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# Abundance of Fish Larvae and Eggs in the Nearshore Area of the Strait of Juan de Fuca, Washington

## Abstract

A quantitative study was made of fish eggs and larvae in the Strait of Juan de Fuca between Angeles Point and Dungeness Spit, Washington, from March through May, 1978. Thirty-three larval taxa represented by 13 fish families were identified during the study. The Family Pleuronectidae contained the largest number of distinct taxa with 11, followed by Cottidae, Stichaeidae, and Liparidae with 10, 5, and 5, respectively. Based on total larval densities for all six sample periods, the most abundant taxa included Pacific herring, unidentified pricklebacks, rockfishes, Pacific sand lances, and unidentified gunnels, with percent relative abundances of 17, 17, 14, 12, and 7 percent, respectively. Maximum larval densities during the six sample periods occurred in late April (385 larvae/100 $m^3$); minimum values were found in early March or May at all stations. The inshore area near Angeles Point (Station 4A) was the most important location in terms of total larval densities and for commercially or recreationally important species such as Pacific herring, codfishes, rockfishes, and flatfishes. Densities of fish eggs were extremely low throughout the study, with a maximum of 17 eggs/100 $m^3$ and a mean of 5 eggs/100 $m^3$ for all samples collected.

## Introduction

The eastern Strait of Juan de Fuca supports a rich fish fauna, important commercial and recreational bottomfish, and salmon fisheries (Washington State Department of Natural Resources, 1974). Important commercial species include true cod, silver salmon, rockfishes, sockeye salmon, pink salmon, and sole; recreational fisheries center on salmon, lingcod, Pacific cod, rockfishes, and kelp greenling. Other fish represent important food items of predatory fish, birds, and mammals in the Strait; these include Pacific herring, sculpins, sea perches, gunnels, longfin smelt, and walleye pollock.

As fishing pressures, industry, and domestic development increase in the Strait, the need to understand fisheries dynamics becomes extremely important. In particular, the possibility of transporting Alaskan Slope oil to refineries or holding facilities in the Strait of Juan de Fuca has prompted descriptions of the type and magnitude of fisheries resources in Port Angeles Harbor and adjacent bays. The present study provides information on the distribution and abundance of ichthyoplankton in the nearshore area between Angeles Point and Dungeness Bay, Washington.

Information on the distribution and occurrence of marine fish larvae and eggs in northern Washington is limited. Most ichthyoplankton studies have been conducted in Puget Sound (Blackburn, 1973; English, 1970; English and Thorne, 1977; Miller *et al.*, 1977; and Waldron, 1972). Miller *et al.* (1977) sampled fish larvae and eggs at 10 locations in northern Puget Sound between February and August, 1976. Other surveys provided information for particular areas such as Skagit Bay (Blackburn, 1973), Port Gardner (English, 1970), and Seattle (English and Thorne, 1977). The only published ichthyoplankton study for the Strait of Juan de Fuca was con-

ducted at nine offshore stations ranging between Cape Flattery and Port Angeles, Washington (Chester *et al.*, 1977). In addition, only limited information exists for adult fish populations in the Strait of Juan de Fuca along the Washington shore (Simenstad *et al.*, 1977).

#### Methods and Materials

Ichthyoplankton stations were set up along four transects, which ranged between Dungeness Bay and Angeles Point (Figure 1). One inshore (10 m depth contour) and one offshore station (30 m depth contour) were established on three transects designated as 1, 2, and 4. Transect 1 was located southeast of Dungeness Spit, Transect 2 was approximately 990 m east of Morse Creek, and Transect 4 was approximately 900 m east of Angeles Point. Only one station, designated as Station 3A, was established on Transect 3, which was located just south of Ediz Hook in Port Angeles Harbor.

Duplicate samples were collected with bongo nets (0.505 mm Nitex mesh; 60 cm mouth diameter) without closing mechanisms. They were collected on a biweekly basis from early March to mid-May, 1978. A time-depth recorder (PKG pinger, Model T-1) was attached to the cable above the bongo nets to record depth and path of tow. In addition, each net was equipped with a General Oceanics flowmeter attached in the mouth to measure the amount of water filtered by the net. The nets were towed along depth contours parallel to shore at a vessel speed of 2-5 knots. A single oblique tow was made along each station contour from near bottom (10 m or 30 m) to the surface. Tow lines ranged between 5 and 17 minutes in duration with a mean value of approximately 8 minutes. Volumes filtered ranged between 55 and 450 $m^3$ with a mean of about 120 $m^3$. Nighttime sampling (between 2100 hr and 0500 hr) was conducted at all stations; daytime sampling was conducted only at Station 2A. All samples were preserved at sea in 5 percent buffered formalin/seawater mixture.

After returning the samples to the laboratory, all fish eggs and larvae were sorted into separate labelled vials containing 5 percent buffered formalin. Larvae and eggs were enumerated and identified to the lowest possible taxon with a Bausch and Lomb stereozoom dissecting microscope. Myomere counts were made with the aid of polarized light. Densities were recorded as the number of larvae or eggs per 100 $m^3$.

The identification of larvae was based in part on the following references: Ahlstrom and Counts (1955), Bolin (1936), Budd (1940), Gorbunova (1962), Hickman (1959), O'Connell (1953), Orcutt (1950), and Pertseva-Ostroumova (1961). Additional taxonomic help was provided by Beverly Vinter and J. Richard Dunn of the Northwest Fisheries Center, National Oceanic and Atmospheric Administration, Seattle, Washington. Voucher specimens and numerous unpublished drawings of larvae compiled at the Northwest Fisheries Center were invaluable in making proper identification.

#### Results and Discussion

A total of 96 samples was examined during six sample periods, which included 12 during the day at Station 2A and 84 during the night at all stations. Thirty-three taxa were identified during the study, representing 13 fish families (Table 1). Of

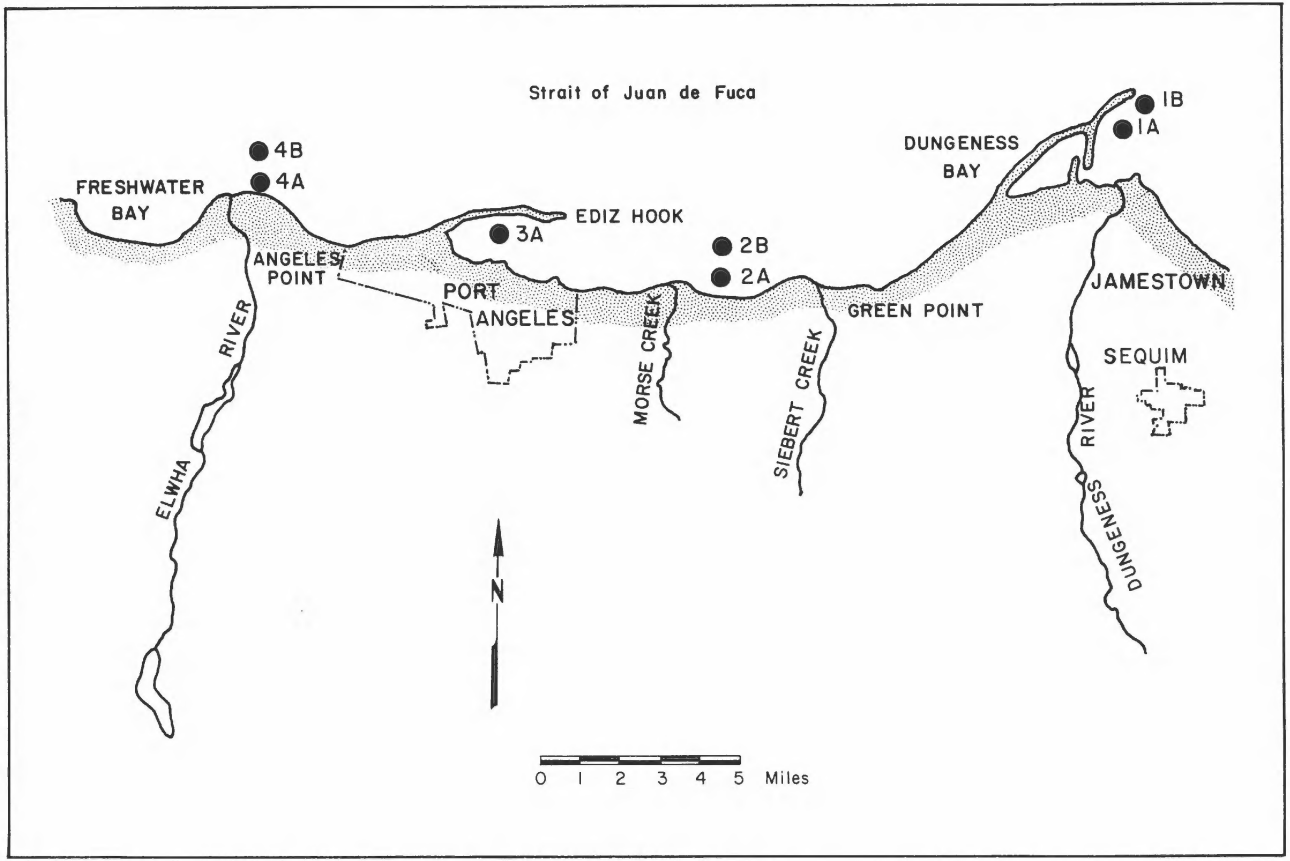


Figure 1. Location of ichthyoplankton sampling stations in the Strait of Juan de Fuca.

these taxa, 27 were identified to genus or species. The Family Pleuronectidae (Right-eye flounders) contained the largest number of distinct taxa with 11, followed by Cottidae (Sculpins), Stichaeidae (Pricklebacks), and Liparidae (Lumpfishes and

TABLE 1. Total densities (number/100 m³), percent relative abundance, and occurrence of fish larvae collected in the Strait of Juan de Fuca between March and May, 1978.

| | | | | Sample Periods | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Scientific Name | Common Name | Total Density | % | 3 Mar | 16 Mar | 29 Mar | 12 Apr | 29 Apr | 12 May |
| Family Agonidae | Poachers | 34.71 | 1.3 | — | D[2] | D | X[3] | X | D |
| Family Ammodytidae | Sand lances | | | | | | | | |
| **Ammodytes hexapterus** | Pacific sand lances | 331.84 | 12.4 | D | X | D | D | D | D |
| Family Bothidae | Lefteye flounders | | | | | | | | |
| **Citharichthys** sp. | Sandab | 0.30 | <0.1 | — | X | — | — | — | — |
| Family Clupeidae | — | | | | | | | | |
| **Clupea harengus pallasi** | Pacific herring | 461.96 | 17.3 | D | D | D | D | D | D |
| Family Cottidae | Sculpins | 168.03 | 6.3 | | | | | | |
| **Artedius** spp. | — | 61.60 | 2.3 | D | D | X | X | D | D |
| **Hemilepidotus spinosus** | Brown irish lord | 0.51 | <0.1 | — | X | — | — | — | — |
| **Icelinus** spp. | — | 6.64 | 0.1 | — | — | — | — | X | X |
| **Leptocottus armatus** | Pacific staghorn sculpin | 2.16 | 0.1 | — | D | — | — | — | X |
| **Radulinus** sp. | — | 6.64 | 0.2 | — | — | — | X | X | X |
| **Scorpanichthys marmoratus** | Carbezon | 14.74 | 0.6 | — | — | — | X | X | X |
| Unidentified cottids | — | 80.58 | 3.0 | — | — | D | D | D | D |
| Family Engraulidae | Anchovies | | | | | | | | |
| **Engraulis mordax** | Northern anchovy | 1.20 | <0.1 | — | — | — | X | — | — |
| Family Gadidae | Codfishes | 212.83 | 7.9 | | | | | | |
| **Gadus macrocephalus/ Microgadus proximus**[1] | Pacific cod/Pacific tomcod | 129.40 | 4.8 | — | X | X | D | D | D |
| **Theragra chalcogramma** | Walleye pollock | 83.43 | 3.1 | — | X | D | D | D | D |
| Family Hexagrammidae | — | 9.98 | 0.4 | | | | | | |
| **Hexagrammos** spp. | Greenlings | 8.01 | 0.3 | D | X | X | X | — | X |
| **Ophiodon elongatus** | Lingcod | 1.97 | 0.1 | — | — | X | X | — | — |
| Family Liparidae | Snailfishes | 70.43 | 2.6 | D | D | D | D | D | D |
| Family Pholidae | Gunnels | 178.49 | 6.7 | D | D | — | X | X | D |
| Family Pleuronectidae | Righteye flounders | 319.02 | 11.9 | | | | | | |
| **Glyptocephalus zachirus** | Rex sole | 13.30 | 0.5 | — | — | X | X | X | X |
| **Hippoglossoides elassodon** | Flathead sole | 7.64 | 0.3 | — | — | — | X | X | X |
| **Isopsetta isolepis** | Butter sole | 30.70 | 1.1 | — | D | X | D | X | D |
| **Lepidopsetta bilineata** | Rock sole | 17.19 | 0.6 | — | X | — | — | D | X |
| **Lyopsetta exilis** | Slender sole | 4.20 | 0.2 | X | X | — | — | X | X |
| **Microstomas pacificus** | Dover sole | 13.55 | 0.5 | — | — | — | X | X | — |
| **Parophrys vetulus** | English sole | 93.15 | 3.5 | — | D | D | D | D | D |
| **Platichthys stellatus** | Starry flounder | 61.37 | 2.3 | X | D | X | D | X | D |
| **Pleuronichthys coenosus** | C-O sole | 1.42 | 0.1 | — | — | — | — | X | X |
| **P. decurrens** | Curlfin sole | 0.89 | <0.1 | — | — | — | — | — | D |
| **Psettichthys melanostictus** | Sand sole | 75.61 | 2.8 | — | D | X | D | X | D |
| Family Scorpaenidae | Scorpionfishes | 369.43 | 13.8 | | | | | | |
| **Sebastes** spp. | Rockfishes | 367.34 | 13.7 | D | D | D | D | D | D |
| **Sebastolobus** sp. | Thornyhead | 2.09 | 0.1 | X | — | — | — | — | — |
| Family Stichaeidae | Pricklebacks | 515.41 | 19.2 | | | | | | |
| **Lyconectes** sp. | — | 67.62 | 2.5 | — | D | D | X | D | — |
| Unidentified stichaeids | — | 447.79 | 16.7 | D | D | D | D | D | D |
| Unidentified larvae | — | 2.93 | 0.1 | — | — | X | X | X | — |

[1]These two species can not be separated at the present time. However, taxonomic descriptions are being processed by Mr. J. Richard Dunn, Northwest Fisheries Center, NOAA, Seattle, Washington.

[2]"D" indicates dominant taxon comprising greater than 5% of the total larval density during a particular sample period.

[3]"X" indicates taxon present in samples collected from at least one station.

Snailfishes) with 10, 5, and 5, respectively. Some families, such as Scorpaenidae (*Sebastes* spp.), probably contained numerous species, but taxonomic difficulties prevented reliable separation. Based on the total larval densities for all six sample periods, the most abundant larval taxa included Pacific herring (*Clupea harengus pallasi*), unidentified pricklebacks (Family Stichaeidae), rockfishes (*Sebastes* spp.), Pacific sand lances (*Ammodytes hexapterus*), and unidentified gunnels (Family Pholidae), with percent relative abundances of 17, 17, 14, 12, and 7 percent, respectively (Table 1). Although particular flounder and cod species represent a small portion of the total larval catch, the families Pleuronectidae and Gadidae were numerically important, comprising 12 and 8 percent of the total density, respectively.

Nineteen taxa were abundant (percent relative abundances greater than 5 percent) at least once between March and May (Table 1). Of these 19 taxa, the dominant or codominant taxa included Pacific herring, Pacific sand lances, Pacific snailfishes (Family Liparidae), unidentified gunnels, unidentified pricklebacks, and unidentified sculpins (Family Cottidae). Most of the dominant larvae occurred throughout the 12-week study; these taxa include Pacific sand lances, Pacific herring, rockfishes, unidentified gunnels, and unidentified pricklebacks (Table 1). In contrast, taxa comprising the families Gadidae, Pleuronectidae, Cottidae, and Hexagrammidae were only common in late March to late April. More detailed seasonal studies in the Pacific Ocean and Puget Sound have shown that most of the larval taxa occurred between March and July (Blackburn, 1973; Richardson and Pearcy, 1977). Species belonging to families such as Bothidae and Osmeridae are more common in, or even restricted to, the fall or winter in northern Pacific waters (Richardson and Pearcy, 1977).

Studies conducted in outer Puget Sound and the Strait of Juan de Fuca reported similar species composition between February and April except for the increased importance of the Family Osmeridae at some locations (Chester *et al.*, 1977; Miller *et al.*, 1977). Although five osmerid species are known to occur in the Strait of Juan de Fuca (Delacy *et al.*, 1972), no smelt larvae were collected in this study. Sampling during the fall or winter probably would have added other species of larvae to the study area.

Quantitative data for the six sample periods are shown in Figure 2. In general, maximum larval densities occurred in late April, while minimum values were found in early March or May. Larval collections in March exhibited considerable variation at the seven stations, with values ranging between 4 and 165 larvae/100 $m^3$. Larval catches in April were considerably higher at all stations. During 12 and 13 April, densities ranged between 19 and 229 larvae/100 $m^3$. Maximum densities for the six sample periods occurred on 29 and 30 April, when abundances were between 43 and 385 larvae/100 $m^3$. The relatively large number of larvae observed in late April was mainly due to increased numbers of Pacific herring, Pacific sand lances, and rockfishes. The final sample period on 12 and 13 May showed that larvae abundances declined with values less than 60 larvae/100 $m^3$ at all stations.

Densities of fish eggs were extremely low throughout the six sample periods with a maximum of 17 eggs/100 $m^3$ and a mean of approximately 5 eggs/100 $m^3$ for all samples collected.

Previous ichthyoplankton studies at deeper locations near Port Angeles reported

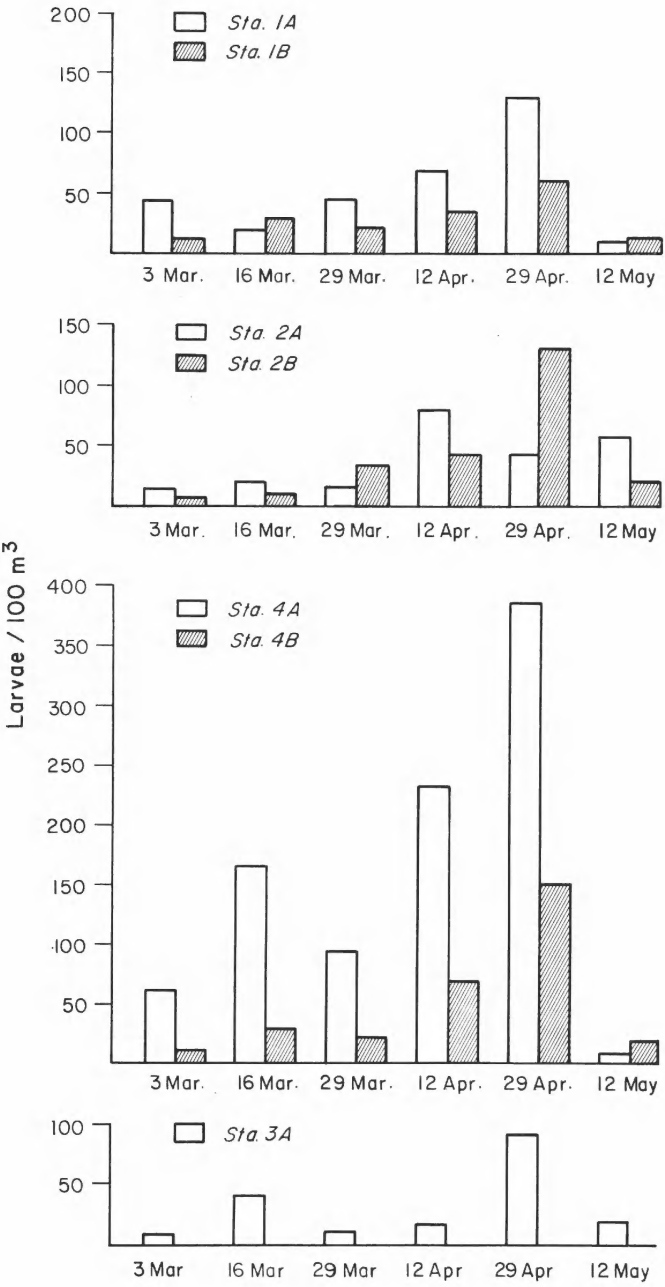


Figure 2. Total larval densities (numbers/100 $m^3$) collected in the Strait of Juan de Fuca between March and April, 1978.

maximum values ranging between 69 and 221 larvae/100 $m^3$ (Chester *et al.*, 1977). Additional ichthyoplankton studies in outer Puget Sound have reported considerably greater densities at some locations where values exceeded 1000 larvae/100 $m^3$ (Miller *et al.*, 1977). The larger standing crops in Puget Sound resulted mainly from Pacific herring.

In general, species composition and larval density varied between the stations. The only consistent pattern was that the inshore station near Angeles Point (Station 4A) supported the greatest larval density for five of the six sample periods. Of the seven stations, Station 4A represented the most important area in terms of total larval numbers and the occurrence of commercially or recreationally important species such as Pacific herring, codfishes, rockfishes, and flatfishes. The largest concentrations of gunnels, Pacific sand lances, and unidentified stichaeids also were found at Station 4A. The lowest larval catches occurred twice each at stations 2B and 3A, and once at stations 2A and 4A. Species composition usually varied between stations on a given sample date (Table 1). Differences in larval composition and density might be explained by density of adult fish species, changes in spawning behavior, current variations, and biological interactions such as predation. Other ichthyoplankton studies in the Strait of Juan de Fuca have demonstrated that the species and density of fish larvae vary considerably among locations. Chester *et al.* (1977) found that April collections near Port Angeles were dominated by cod, sand lances, sculpins, and pricklebacks, while flatfishes and smelt were the most abundant families near Cape Flattery.

Diurnal differences in larval densities were investigated at Station 2A. Daytime collections contained greater densities for five of six sample periods (Figure 3). During three sample periods (3 March, 16 March, 12 April) densities in daytime collections were approximately twice as large as in nocturnal collections. Pricklebacks were the dominant larvae in the daytime samples, but occurred in minimal numbers at night. Numerous studies have reported that nighttime samples usually yielded the greatest larval densities (e.g., Bridger, 1956; Eldridge, 1977; Richardson and Pearcy, 1977; UNESCO, 1975). In an attempt to explain the diurnal distribution of fish larvae in Richardson Bay, California, Eldridge (1977) found a positive correlation between

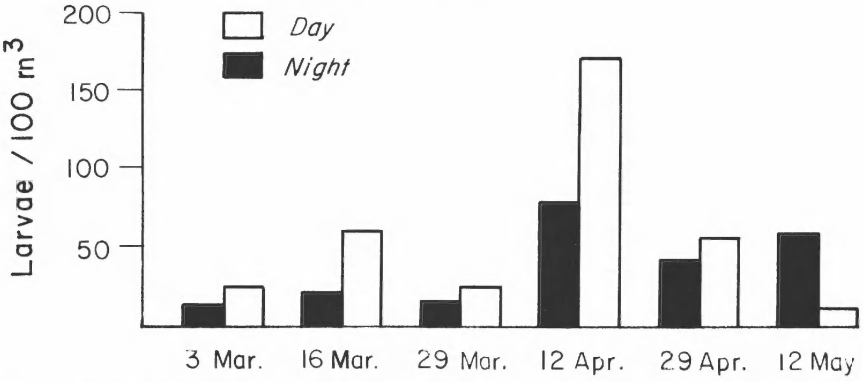


Figure 3. Larval densities (numbers/100 $m^3$) during day and night sampling at Station 2A in the Strait of Juan de Fuca between 3 March and 12 May 1978.

tidal currents and density. The highest larval densities occurred when tidal currents were the fastest. Other factors which may influence day-night distributions of ichthyoplankton include extent of cloud cover (light), behavior of larvae, and sampling methodologies. The depth also may affect day-night distributions. Blackburn (1973) sampled shallow areas (5-18 m) in Skagit Bay, Washington, and found variable and inconsistent larval fish densities in day and night tows. The present study area was shallow; in contrast, daytime collections yielded greater densities than nighttime samples during most of the study period. Obviously, more information is needed to identify the important factors influencing the diurnal distributional changes of ichthyoplankton.

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# Uranium Concentration in the Ground Waters of the Pullman-Moscow Basin, Whitman County, Washington, and Latah County, Idaho

## Abstract

Uranium concentration in the ground waters of the Pullman-Moscow basin was determined using a high-sensitivity nuclear track technique. The limit of detection was calculated as 5 parts-per-trillion.

The spatial distribution of uranium in the ground waters of the Pullman-Moscow basin shows clusters of high concentration along the eastern edges of the basin in close proximity to the granodiorite of the Thatuna batholith. This phenomenon is probably related to the Moscow sub-basin recharge area, where oxidizing surface waters are leaching uranium from the surrounding granitic rocks. Very low uranium concentrations are generally associated with deep, high-yield municipal and domestic wells in the central and western parts of the basin. This observation probably relates to reducing conditions in the deep ground water environment of the Pullman-Moscow basin.

## Introduction

The Pullman-Moscow basin is located in the southeastern part of Whitman County, Washington, and west-central Latah County, Idaho. It is situated about 80 mi (128 km) south of Spokane, Washington, on U.S. Highway 195. The basin is surrounded by topographic highs consisting of pre-Tertiary age quartzites and granites such as Kamiak Butte and the Palouse Range on the north and east, and Tomer Butte, Paradise Ridge, and Bald Butte on the south, respectively. Most of these features lie off the edge of Figure 1. The lowlands of this region consist of flat-lying basalts of the Columbia River Group overlain by wind-deposited silt of the Palouse formation. The basin is 20 mi (32.1 km) long and 15 mi (24.2 km) wide at the widest location and encloses an area of 250 sq mi (647.7 $km^2$).

There are two major population centers located within this basin. Moscow, Idaho, which has a population of 15,500, is situated in the eastern portion of the basin 2 mi (3.2 km) from the Washington-Idaho State Line. Pullman, Washington, with a population of 24,500, is about 8 mi (12.8 km) west of Moscow. Most of the area consists of scattered wheat farms, grassland, and woodland.

## Purpose

This study was conducted in order to determine the concentration of dissolved uranium in the ground waters of the Pullman-Moscow basin. The work also involved comparisons of conductivity and pH to uranium concentrations, and the relationships of

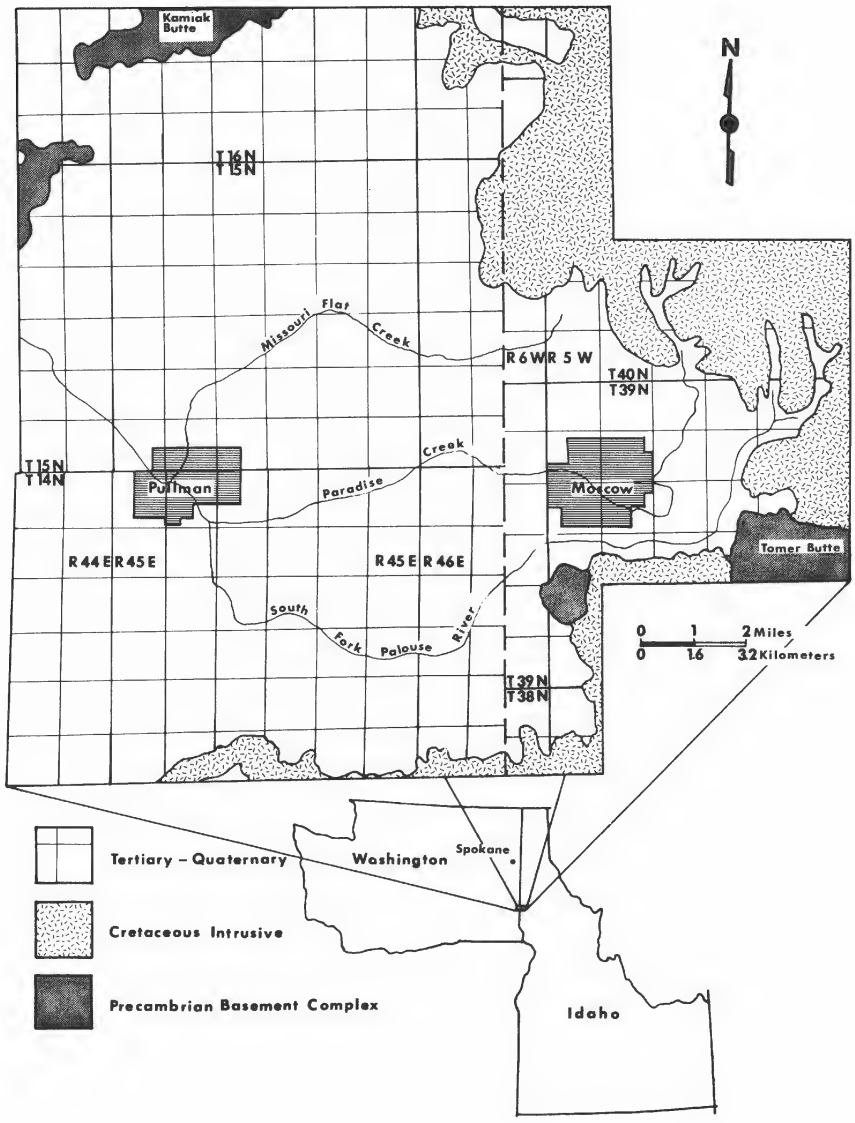


Figure 1. Location map of the Pullman-Moscow basin (from Ichimura, 1978).

these parameters to basin hydrogeochemistry.

Research was inspired by the recent increase of uranium exploration, and an earlier unpublished finding of anomolously high radiation background in samples of basin ground water when age dating was attempted. This latter finding suggested

that uranium might be present in higher-than-normal-trace quantities, and that the high background counts might be related to uranium daughter products in solution.

### Geology

The pre-Tertiary rocks can be classified into two groups in the Pullman-Moscow basin. The oldest are of Precambrian age (700 my) and consist primarily of quartzites which are probably part of the Belt Supergroup and correlative with the Revett formation of the Ravalli Group (Savage, 1973). Granitic intrusives of the Thatuna batholith comprise the second group of rocks. Their approximate age is late Jurassic or early Cretaceous (130 my) (Eardley, 1962). Textural features, composition, and age similarities indicate that the Thatuna batholith is probably a westward extension of the Idaho batholith.

By late Miocene time, an erosional surface consisting of pre-Tertiary rocks with deep broad valleys and relief of at least 3000 ft (914 m) had formed in this area. Basalt flows from fissure-type eruptions to the west flooded this surface, damming some of the drainage valleys and forming lakes and swamps in which deposits of gravel, sand, and silt accumulated. Repeated floods of basalts, followed by periods of erosion, formed the intercalated "Latah" formation[1]—Columbia River Basalt stratigraphy of the Pullman-Moscow basin (Figure 2). Regional subsidence accompanying the later basalt eruptions led to the formation of gentle warps and other minor structures in the basalt (Waters, 1961). During the middle to late Pleistocene (1-2 my), after

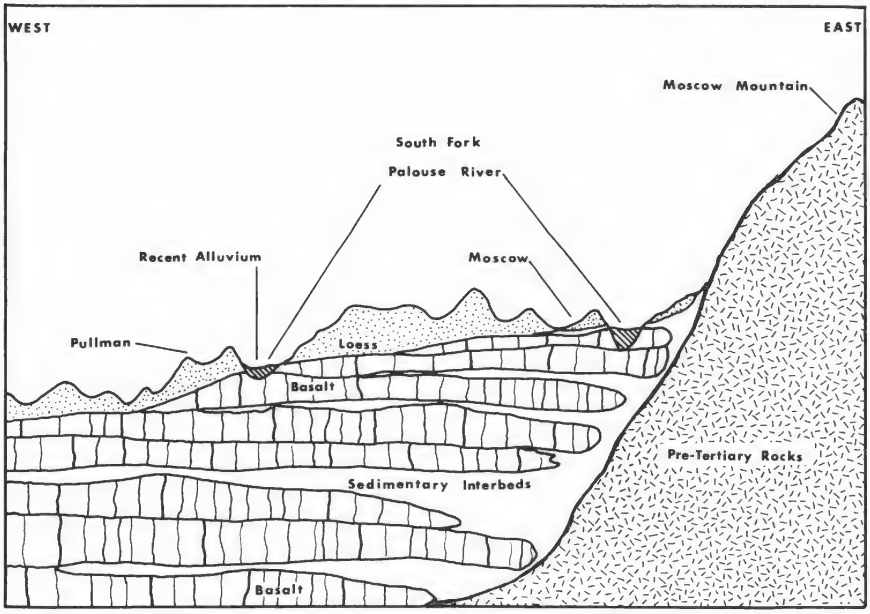


Figure 2. Schematic geologic section through the Pullman-Moscow basin (from Ichimura, 1978).

[1]"Latah" formation is the name used for all sedimentary interbeds associated with erosional periods which stratigraphically underlie or are between or immediately overlie the Columbia River Group. It is not a formation in true stratigraphic sense.

the last basalt eruptions, wind-transported silt of the Palouse formation loess was deposited to form the low relief, rolling-hill lowlands.

#### Ground Water

The physiographic basin and lithology define the ground-water divide on the north, south, and east. Therefore, recharge to the basin flows westward toward the Snake River Canyon. Ground water recharge for the Moscow area is thought to occur primarily along the contact between the basalts and the crystalline rocks in the basin (Lin, 1967; and Laney *et al.*, 1923). However, recharge in the Pullman area is probably occurring throughout the overlying loess and basalt, especially along stream beds, joints, and clastic dikes (Foxworthy and Washburn, 1963).

Most domestic ground waters are obtained from wells greater than 150 feet deep which tap confined basalt aquifers. The upper parts of most basalt flows are relatively permeable because of the occurrence of vesicles, fractures, and weathered materials. Large wells are capable of yielding 1800 gm (113 liters/sec) or more when several aquifers are penetrated. Small to moderate quantities (100 gpm or less) of water are derived from wells tapping relatively coarse-grained sedimentary interbeds of the Moscow area. However, similar beds contribute only minor amounts of water in the Pullman area. The surficial Palouse formation is an important source of domestic and stock water in the rural areas. In general, water well yields from the Palouse formation are less than 1.0 gpm (0.06 liter/sec). Many of these shallow Palouse formation wells dry up during the late summer. Unweathered granite and metamorphic rocks are poor aquifers whereas the weathered granitic and metamorphic rocks are found to be mediocre aquifers if interstitial clays are minimal.

#### Uranium Geology and Hydrogeochemistry

Uranium and thorium tend to occur together naturally in average uranium to thorium ratios of about 1 to 4. Based on meteorite standards and heat-flow geophysical information, uranium and thorium are thought to be enriched by a factor of 200 and 230, respectively, in the crust; they are depleted, accordingly, in the deeper sections of the earth. Radiochemical analyses indicate low concentrations of uranium and thorium in mafic peridotites and pyrolites of the upper mantle, and maximum enrichments of 400 and 500 times for uranium and thorium, respectively, in granite (Green and Ringwood, 1963; and Gabelman, 1977). Basalts and ultramafic rocks are characteristically low in uranium.

Uranium and thorium atoms do not fit well within most silicate structures; hence, a large fraction tend to remain free to migrate with the last remaining volatiles of an intrusive body. Therefore, uranium and thorium have been associated most frequently with post-magmatic hydrothermal emanations. Such behavior causes much of the uranium and thorium to be trapped as intergranular coatings in a manner that makes uranium more accessible to water leaching (Roshold *et al.*, 1973).

Uranium concentrations in ground waters vary over broad ranges. Dissolved sexivalant ions range from 20 ppb (parts-per-billion) to 1.5 ppb in fresh waters of the Colorado Plateau to average lows of 0.3 ppb in the ground waters of Illinois. Parts-per-million levels of uranium in ground waters can be found in mineralized zones containing parts-per-hundred uranium concentrations (Gabelman, 1977). Most

natural surface and ground waters have concentrations in the few parts-per-billion range. However, in general, concentrations vary widely in the same drainage area or aquifer in response to local changes in pH, Eh, and temperature (Davis and De Wiest, 1966).

There are two major uranium mines in the general vicinity of the Pullman-Moscow basin. The Midnite Mine is located 35 air mi (56.3 km) northwest of Spokane, on the Spokane Indian Reservation, Stevens County, Washington. It is one of two mines in the United States currently producing uranium from discordant contacts in crystalline host rocks (Nash and Lehman, 1975). The nearby Sherwood Mine is being developed in the pre-Eocene "Latah-like" sedimentary beds, and is located approximately 5 mi (8.1 km) south of the Midnite Mine. The sediments in the area of the Sherwood ore body are primarily arkosic, poorly sorted sandstones, indicative of high-energy sedimentary deposition. The lignite seams associated with the deposit are indicative of reducing conditions which probably served as a fixation mechanism for the uranium (Veelick, 1977).

The geology of the Sherwood Mine area is similar to the Pullman-Moscow basin. According to popular belief, the probable source rock is a Cretaceous (40 my) quartz monzonite (ademellite) pluton adjacent to the ore body. The Columbia River Basalt overlying most of the deposit acted as a "cap" rock which protected the deposit from surficial erosion. According to Veelick (1977), the estimated age of this particular deposit is pre-Eocene to Cretaceous (10 to 40 my). Therefore, based on the popular laterogene theory of formation of sedimentary uranium deposits, in which uranium leached from a weathering pluton by ground water is transported and mineralized in the surrounding sedimentary media, the "Latah" formation interbeds and their pre-Eocene counterparts of the Pullman-Moscow basin appear to be a likely host for a uranium deposit. In addition to a potential source (Thatuna batholith), fixation mechanisms indicative of a reducing environment, such as preserved organic matter, are commonly noted in well cuttings of the eastern part of the Pullman-Moscow basin.

#### Sampling and Analytical Methods

Ground water sampling procedures included on-site temperature, pH, and conductivity measurements. Most of these measurements were made during the summer and fall of 1976. On-site measurements and sampling operations were conducted after 5 min of pumping whenever possible. Water samples were stored for a maximum of 5 hrs in 500 ml polyethylene bottles before being processed in the laboratory. This practice minimized bottle wall sorption of trace uranium from solution (Ichimura, 1978).

The nuclear track technique was chosen as the analytical method in this project because of its sensitivity for measuring low uranium concentration, and its independence from interference from other elements. Limit of detection was measured to be about 5 ppt (parts-per-trillion) for naturally occurring uranium containing 0.711 percent $^{235}U$ (Ichimura, 1978).

In summary, the analytical method requires 0.10 ml of water sample pipetted and evaporated in a specially designed acid-washed polyethylene dish (Figure 3). A clean mica (track detector) with low uranium concentration was placed in a slot over the remaining residue in the central depression. A number of dishes, with some containing known concentrations of uranium (standards), and others for background

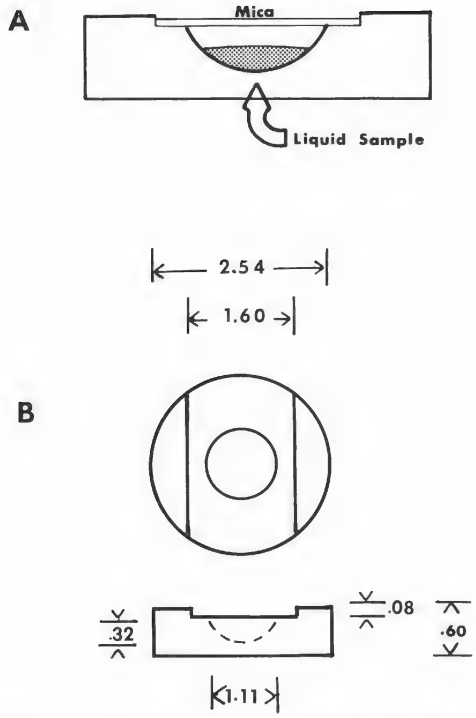


Figure 3. Sample dish configuration for uranium analysis by the fission track technique. (A) Shaded area shows approximate location of the sample before evaporation; (B) Dish dimensions in centimeters (from Ichimura, 1978).

determination containing no added uranium (blanks), were prepared in a similar manner and stacked one upon the other to make a sample set. Each sample set was irradiated simultaneously with the same fluence of thermal neutrons in a TRIGA type nuclear reactor for a maximum of 8 hrs at 1 megawatt ($5.0 \times 10^{12}$ neutrons/$cm^2$–sec). During the irradiation process, thermal neutrons impinging upon $^{235}U$ atoms causes them to fission with known probability and a known fraction of the fission fragments collided with the mica surface. These collisions created sub-microscopic damage paths (latent tracks) about 50 angstroms in diameter and 14 microns long in the crystalline structure of the mica. After a cooling period of about 10 days, the mica pieces were removed from the polyethylene containers and etched in a bath of hydrofluoric acid for 30 mins at room temperature (23°C). The etch rate of the mica is greatly enhanced along the damage paths intersecting the mica surface and the submicroscopic damage paths are enlarged. These damage paths are later observed under an optical microscope at 400x. The observed track density (tracks/$cm^2$) is proportional to the concentration of uranium in a given sample (Figure 4).

The nuclear track technique has a number of advantages and drawbacks (Ichimura, 1978). Evaporating a sample in a dish eliminates sorption losses and relieves the sampler of the task of carrying large quantities of liquid samples to the laboratory.

Figure 4. Fission tracks magnified 400x. Tracks are about 14 microns long (from Ichimura, 1978).

Interferences from common elements are absent, and if the track density is too high to be counted under a microscope because of abnormally high uranium concentration, a new detector (mica) can be mounted on the dish and reirradiated with negligible error. Experiments confirmed that fast neutron fission of $^{232}Th$ was negligible, eliminating the possibility of thorium interference (Ichimura, 1978). The requirement of an intense neutron source (nuclear reactor) and the radiation resulting from irradiation activation are disadvantages of the method.

#### Results and Discussion

Table 1 lists 129 sample results with supporting data from various parts of the Pullman-Moscow basin. The data include uranium concentration in parts-per-billion, observed error of one standard deviation in ppb, pH, conductivity in micromhos at 25°C, and sample location. In all cases, sample locations are given as W for Washington, township north, range east, and section number, and I for Idaho, township north, range west, and section number. Some identical samples are found in Table 1 because a few wells were sampled a number of times to study the reliability of a single field measurement. Data appear to show good reproducibility or within 35 percent.

The shaded areas in Figure 5 define regions containing sample points having uranium concentrations greater than 1.0 ppb and separated by less than 1.0 air mi (1.6 km). In all cases, these regions were near the edge of the basin and on, or near, the basalt-intrusive rock contact. The assays from samples in the middle of the basin

TABLE 1. List of results from geochemical survey in the Pullman-Moscow basin.

| Code | Amount (ppb) | Error (+/-ppb) | pH | Cond (U-mho) | Depth (Ft) | Location |
|---|---|---|---|---|---|---|
| A- 2 | 0.394E-01 | 0.149E-01 | 6.60 | 0.0 | 560 | I-39/ 5- 7 |
| A- 6 | 0.853E-02 | 0.350E-02 | 7.90 | 0.0 | 1305 | I-39/ 5- 8 |
| A- 8 | 0.480E-01 | 0.177E-01 | 6.10 | 0.0 | 1500 | I-39/ 5- 7 |
| B- 1 | N. D. | N. D. | 7.70 | 340.0 | 396 | W-15/45-34 |
| B- 2 | 0.166E-01 | 0.652E-02 | 8.20 | 350.0 | 247 | W-14/45- 5 |
| B- 3 | N. D. | N. D. | 8.00 | 315.0 | 214 | W-14/45- 5 |
| B- 4 | N. D. | N. D. | 7.80 | 335.0 | 223 | W-14/45- 5 |
| B- 5 | N. D. | N. D. | 7.90 | 350.0 | 275 | W-14/45- 5 |
| B- A | 0.235E-01 | 0.928E-02 | 7.40 | 330.0 | 0 | I-39/ 5- 7 |
| C- 1 | 0.585E 00 | 0.182E 00 | 6.80 | 290.0 | 200 | I-39/ 6-27 |
| C- 2 | 0.514E 00 | 0.165E 00 | 6.90 | 310.0 | 85 | I-39/ 5-22 |
| C- 3 | 0.868E 00 | 0.261E 00 | 6.20 | 310.0 | 106 | I-39/ 6-26 |
| C- 4 | 0.791E 00 | 0.239E 00 | 6.40 | 300.0 | 164 | I-39/ 6-27 |
| C- 5 | 0.899E 00 | 0.267E 00 | 5.80 | 400.0 | 35 | I-39/ 5-15 |
| C- 6 | 0.551E-01 | 0.209E-01 | 6.30 | 305.0 | 0 | I-39/ 6-27 |
| C- 7 | 0.410E 00 | 0.134E 00 | 6.60 | 290.0 | 0 | I-39/ 5-22 |
| C- 8 | N. D. | N. D. | 6.70 | 270.0 | 160 | I-39/ 5-15 |
| D- 1 | 0.671E 00 | 0.235E 00 | 6.20 | 385.0 | 102 | I-39/ 5-22 |
| D- 2 | 0.163E-01 | 0.768E-02 | 6.40 | 480.0 | 210 | I-39/ 5-22 |
| D- 3 | 0.483E 00 | 0.186E 00 | 6.70 | 385.0 | 210 | I-39/ 5-16 |
| D- 4 | 0.575E 00 | 0.215E 00 | 6.90 | 375.0 | 190 | I-39/ 5-20 |
| D- 5 | 0.800E 00 | 0.289E 00 | 7.00 | 340.0 | 223 | I-39/ 6-28 |
| D- 6 | 0.102E 00 | 0.444E-01 | 6.60 | 375.0 | 50 | I-39/ 5-21 |
| D- 7 | 0.899E 01 | 0.253E 01 | 6.80 | 731.0 | 0 | I-39/ 5-20 |
| E- 1 | 0.784E 01 | 0.209E 01 | 6.30 | 330.0 | 0 | I-39/ 5-11 |
| E- 2 | 0.170E 00 | 0.692E-01 | 6.20 | 365.0 | 26 | I-39/ 5- 2 |
| E- 3 | 0.272E 01 | 0.848E 00 | 6.70 | 320.0 | 90 | I-39/ 5-12 |
| E- 4 | 0.256E 01 | 0.805E 00 | 6.90 | 300.0 | 190 | I-39/ 5- 1 |
| E- 5 | 0.309E 00 | 0.120E 00 | 7.00 | 330.0 | 125 | I-39/ 5-14 |
| E- 6 | 0.103E 01 | 0.364E 00 | 6.80 | 330.0 | 400 | I-39/ 5- 1 |
| E- 7 | 0.861E-01 | 0.371E-01 | 6.50 | 230.0 | 200 | I-39/ 5-11 |
| F- 2 | 0.340E 00 | 0.126E 00 | 7.10 | 360.0 | 252 | I-39/ 5-15 |
| F- 3 | 0.392E 00 | 0.144E 00 | 6.80 | 320.0 | 155 | I-39/ 5-15 |
| F- 4 | 0.296E-01 | 0.132E-01 | 7.30 | 390.0 | 1500 | I-39/ 5- 7 (A-8) |
| F- 5 | 0.525E 01 | 0.151E 01 | 7.20 | 190.0 | 240 | I-40/ 5-25 |
| F- 6 | 0.140E 01 | 0.466E 00 | 7.40 | 430.0 | 290 | I-40/ 5-36 |
| F- 7 | 0.381E 00 | 0.144E 00 | 6.50 | 200.0 | 92 | I-40/ 6-31 |
| G- 1 | 0.176E 00 | 0.685E-01 | 6.70 | 220.0 | 80 | I-40/ 5-34 |
| G- 2 | 0.728E 00 | 0.250E 00 | 6.50 | 230.0 | 0 | I-40/ 5-25 |
| G- 3 | 0.312E 00 | 0.116E 00 | 6.60 | 175.0 | 60 | I-40/ 5-26 |
| G- 4 | 0.108E 02 | 0.283E 01 | 7.10 | 510.0 | 250 | I-39/ 4- 6 |
| G- 5 | 0.114E 01 | 0.369E 00 | 6.10 | 160.0 | 64 | I-40/ 5-25 |
| G- 6 | 0.389E 01 | 0.112E 01 | 7.10 | 270.0 | 0 | I-39/ 5- 1 |
| G- 7 | 0.147E 01 | 0.475E 00 | 6.70 | 205.0 | 200 | I-40/ 5-36 |
| G- 8 | 0.161E 01 | 0.507E 00 | 6.70 | 200.0 | 0 | I-40/ 6-31 |
| H- 1 | 0.313E 00 | 0.978E-01 | 6.40 | 280.0 | 75 | I-39/ 5- 9 |
| H- 2 | 0.755E-01 | 0.263E-01 | 6.20 | 140.0 | 135 | I-39/ 5- 2 |
| H- 3 | 0.171E 01 | 0.420E 00 | 6.70 | 520.0 | 65 | I-39/ 5- 2 |
| H- 4 | 0.625E 00 | 0.176E 00 | 6.90 | 460.0 | 50 | I-39/ 5- 4 |
| I- 1 | 0.465E 00 | 0.168E 00 | 6.20 | 180.0 | 0 | I-40/ 5-24 |
| I- 2 | 0.344E 00 | 0.126E 00 | 6.40 | 300.0 | 0 | I-40/ 5-23 |
| I- 3 | 0.988E-01 | 0.395E-01 | 5.90 | 120.0 | 10 | I-40/ 5-15 |
| I- 4 | 0.244E 01 | 0.753E 00 | 6.10 | 210.0 | 100 | I-40/ 5-23 |
| I- 5 | 0.149E 00 | 0.586E-01 | 6.00 | 140.0 | 0 | I-40/ 5-23 |
| I- 6 | 0.216E 01 | 0.658E 00 | 6.70 | 310.0 | 305 | I-40/ 5-26 |
| I- 7 | 0.234E 00 | 0.890E-01 | 6.50 | 185.0 | 10 | I-40/ 5-26 |
| I- 8 | 0.790E 00 | 0.265E 00 | 6.60 | 95.0 | 0 | I-40/ 5-23 |

| | | | | | | |
|---|---|---|---|---|---|---|
| J- 1 | 0.130E 01 | 0.421E 00 | 6.20 | 225.0 | 155 | I-40/ 5-23 |
| J- 2 | N. D. | N. D. | 6.40 | 95.0 | 130 | I-40/ 5-27 |
| J- 3 | 0.140E 00 | 0.551E-01 | 5.90 | 160.0 | 0 | I-40/ 5-17 |
| J- 4 | 0.304E 01 | 0.894E 00 | 6.50 | 180.0 | 0 | I-39/ 5- 5 |
| J- 5 | 0.781E-01 | 0.312E-01 | 6.30 | 165.0 | 0 | I-40/ 5-29 |
| J- 6 | N. D. | N. D. | 6.50 | 175.0 | 0 | I-40/ 5-21 |
| J- 7 | 0.120E 01 | 0.390E 00 | 7.10 | 260.0 | 0 | I-40/ 5- 8 |
| J- 8 | 0.224E 01 | 0.690E 00 | 7.50 | 320.0 | 0 | I-40/ 5- 8 |
| J- 9 | 0.194E 00 | 0.745E-01 | 6.50 | 350.0 | 90 | I-40/ 5-32 |
| K- 1 | 0.235E 01 | 0.558E 00 | 6.90 | 300.0 | 246 | I-40/ 5-20 |
| K- 2 | 0.408E-01 | 0.157E-01 | 6.10 | 360.0 | 60 | I-40/ 5-19 |
| K- 3 | 0.525E 01 | 0.110E 01 | 6.50 | 600.0 | 0 | I-40/ 5-18 |
| K- 4 | 0.226E-01 | 0.904E-02 | 6.20 | 425.0 | 231 | I-40/ 5-30 |
| K- 5 | 0.104E 00 | 0.362E-01 | 5.90 | 440.0 | 38 | I-40/ 5-29 |
| K- 6 | 0.297E 01 | 0.722E 00 | 6.50 | 180.0 | 412 | I-40/ 5-18 |
| K- 7 | 0.189E 00 | 0.624E-01 | 6.50 | 220.0 | 0 | I-40/ 5-19 |
| L- 1 | 0.113E 01 | 0.304E 00 | 6.70 | 305.0 | 58 | W-15/46-20 |
| L- 2 | 0.414E-01 | 0.158E-01 | 6.90 | 520.0 | 60 | I-40/ 5-32 |
| L- 3 | 0.690E-01 | 0.254E-01 | 6.50 | 400.0 | 270 | I-39/ 5- 5 |
| L- 4 | 0.310E 00 | 0.979E-01 | 6.70 | 245.0 | 118 | I-30/ 5- 5 |
| L- 5 | 0.287E 00 | 0.936E-01 | 6.40 | 290.0 | 23 | I-40/ 5-31 |
| L- 6 | 0.438E-01 | 0.166E-01 | 6.60 | 400.0 | 68 | I-39/ 5- 6 |
| L- 7 | N. D. | N. D. | 6.90 | 305.0 | 320 | I-40/ 5-31 |
| L- 8 | 0.377E-01 | 0.143E-01 | 6.50 | 300.0 | 204 | I-40/ 6-26 |
| M- 1 | 0.549E 01 | 0.128E 01 | 6.50 | 610.0 | 90 | I-39/ 5- 5 |
| M- 2 | 0.861E 00 | 0.245E 00 | 6.70 | 305.0 | 376 | I-39/ 5- 6 |
| M- 3 | N. D. | N. D. | 7.40 | 320.0 | 223 | W-14/45- 5 (B-4) |
| M- 4 | N. D. | N. D. | 7.60 | 320.0 | 396 | W-15/45-34 (B-1) |
| M- 5 | 0.247E 00 | 0.819E-01 | 6.80 | 395.0 | 106 | I-39/ 5-19 |
| M- 6 | 0.228E 01 | 0.601E 00 | 7.30 | 325.0 | 68 | I-39/ 5-19 |
| N- 1 | 0.701E-01 | 0.251E-01 | 6.30 | 315.0 | 0 | I-39/ 6-24 |
| N- 2 | 0.960E 01 | 0.196E 01 | 6.30 | 800.0 | 20 | I-39/ 5-20 (D-7) |
| N- 3 | 0.511E 00 | 0.152E 00 | 6.60 | 300.0 | 0 | I-39/ 5-19 |
| N- 4 | 0.268E 01 | 0.654E 00 | 7.30 | 315.0 | 380 | I-39/ 6-30 |
| N- 5 | 0.808E 00 | 0.235E 00 | 7.50 | 240.0 | 200 | I-39/ 5-22 |
| N- 6 | 0.249E 02 | 0.519E 01 | 6.70 | 445.0 | 0 | I-39/ 6-30 |
| N- 7 | 0.284E 00 | 0.912E-01 | 6.40 | 220.0 | 16 | I-39/ 5-22 |
| N- 8 | 0.928E 00 | 0.257E 00 | 7.50 | 275.0 | 225 | I-39/ 5-22 |
| O- 1 | 0.117E 01 | 0.312E 00 | 6.20 | 330.0 | 16 | I-39/ 5-10 |
| O- 2 | 0.116E 01 | 0.306E 00 | 6.60 | 315.0 | 295 | I-39/ 5-16 |
| O- 3 | 0.515E 00 | 0.150E 00 | 6.60 | 265.0 | 45 | I-39/ 5- 4 |
| O- 4 | 0.343E 00 | 0.106E 00 | 6.80 | 295.0 | 0 | I-39/ 5- 4 |
| O- 5 | 0.333E 01 | 0.748E 00 | 6.30 | 740.0 | 30 | I-39/ 5- 9 |
| O- 6 | 0.101E 01 | 0.268E 00 | 6.60 | 265.0 | 60 | I-39/ 5-10 |
| O- 7 | 0.170E 00 | 0.565E-01 | 6.60 | 210.0 | 275 | I-39/ 5-10 |
| P- 1 | 0.140E 01 | 0.371E 00 | 7.00 | 415.0 | 15 | W-16/45-26 |
| P- 2 | 0.768E 00 | 0.222E 00 | 7.00 | 305.0 | 0 | W-16/45-35 |
| P- 3 | 0.173E 01 | 0.445E 00 | 6.90 | 355.0 | 125 | W-15/45- 1 |
| P- 4 | 0.442E-02 | 0.170E-02 | 7.40 | 295.0 | 30 | W-15/45-18 |
| P- 5 | 0.137E 01 | 0.361E 00 | 6.50 | 200.0 | 0 | W-15/46- 7 |
| P- 6 | 0,262E-03 | 0.101E-03 | 6.20 | 145.0 | 60 | I-40/16-24 |
| P- 7 | 0.436E 00 | 0.130E 00 | 6.70 | 270.0 | 123 | W-15/45- 8 |
| P- 8 | 0.336E 00 | 0.103E 00 | 6.80 | 260.0 | 107 | W-16/45-32 |
| Q- 1 | 0.726E-01 | 0.264E-01 | 7.20 | 280.0 | 285 | W-15/45-14 |
| Q- 2 | 0.541E 00 | 0.155E 00 | 6.40 | 570.0 | 250 | W-15/46-20 |
| Q- 3 | 0.184E 00 | 0.604E-01 | 6.80 | 245.0 | 125 | W-14/45- 2 |
| Q- 4 | 0.195E 00 | 0.637E-01 | 7.00 | 230.0 | 150 | W-15/45-28 |
| Q- 5 | 0.336E 00 | 0.102E 00 | 7.00 | 265.0 | 435 | W-15/45-26 |
| Q- 6 | 0.971E-01 | 0.337E-01 | 6.70 | 235.0 | 120 | W-15/45-26 |
| Q- 7 | 0.173E 01 | 0.447E 00 | 6.80 | 410.0 | 205 | W-14/45- 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| R- 1 | 0.298E 00 | 0.103E 00 | 6.80 | 275.0 | 212 | W-14/46- 6 |
| R- 2 | 0.404E 00 | 0.131E 00 | 7.00 | 240.0 | 264 | W-15/45-25 |
| R- 3 | 0.120E 01 | 0.375E 00 | 7.20 | 320.0 | 80 | W-14/46-19 |
| R- 4 | 0.195E 01 | 0.565E 00 | 6.90 | 310.0 | 130 | W-14/45-28 |
| R- 5 | 0.529E 00 | 0.160E 00 | 6.50 | 320.0 | 128 | W-14/45-29 |
| R- 6 | 0.326E 00 | 0.108E 00 | 6.80 | 240.0 | 6 | W-14/46-20 |
| S- 1 | 0.481E 00 | 0.149E 00 | 6.70 | 200.0 | 116 | W-15/45- 9 |
| S- 2 | 0.324E 00 | 0.104E 00 | 7.20 | 240.0 | 340 | W-15/45-20 |
| S- 3 | 0.239E 01 | 0.686E 00 | 7.00 | 310.0 | 55 | W-16/45-27 |
| S- 4 | N. D. | N. D. | 7.20 | 240.0 | 152 | W-14/45- 3 |
| S- 6 | 0.213E-01 | 0.826E-02 | 6.60 | 240.0 | 492 | I-39/ 5-15 |
| S- 7 | 0.926E-02 | 0.368E-02 | 7.60 | 270.0 | 371 | W-15/45-30 |

N. D. equals no detection.

pH, conductivity, depth zero (0) means no data obtained during sampling.
Conductivity is measured in micromhos-per-centimeter at 25 degrees centigrade.

Location code is defined as followed: state, W=Washington, I=Idaho - township, north/range west (Idaho), east (Washington) - section.

generally contained lower uranium concentrations. With the exceptions of samples S-3 and P-1 in the northwest part of the basin, the clusters of high uranium concentrations in the southeast, east and south portions of the basin all correspond to possible recharge areas of the Moscow sub-basin (Lin, 1967), where most of the wells penetrate decomposed granites. It is proposed that oxidizing meteoric waters are recharging the basin and leaching uranium from the granitic rocks at these localities.

The highest recorded uranium concentration, sample N-6 which assayed 25 ppb uranium, was located in the southern part of the Moscow sub-basin near granitic rocks containing smoky quartz crystals.

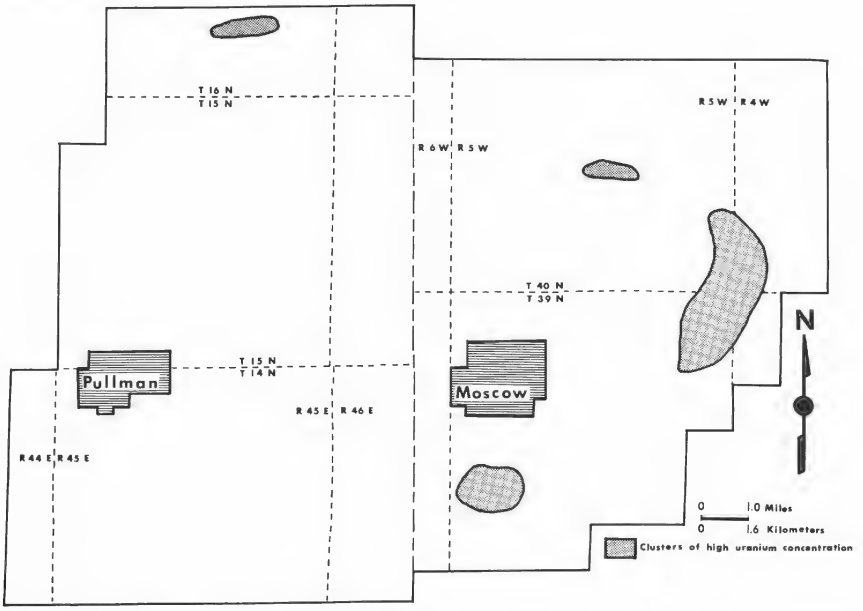


Figure 5. Geochemical survey map showing high uranium concentration in the Pullman-Moscow basin (modified from Ichimura, 1978).

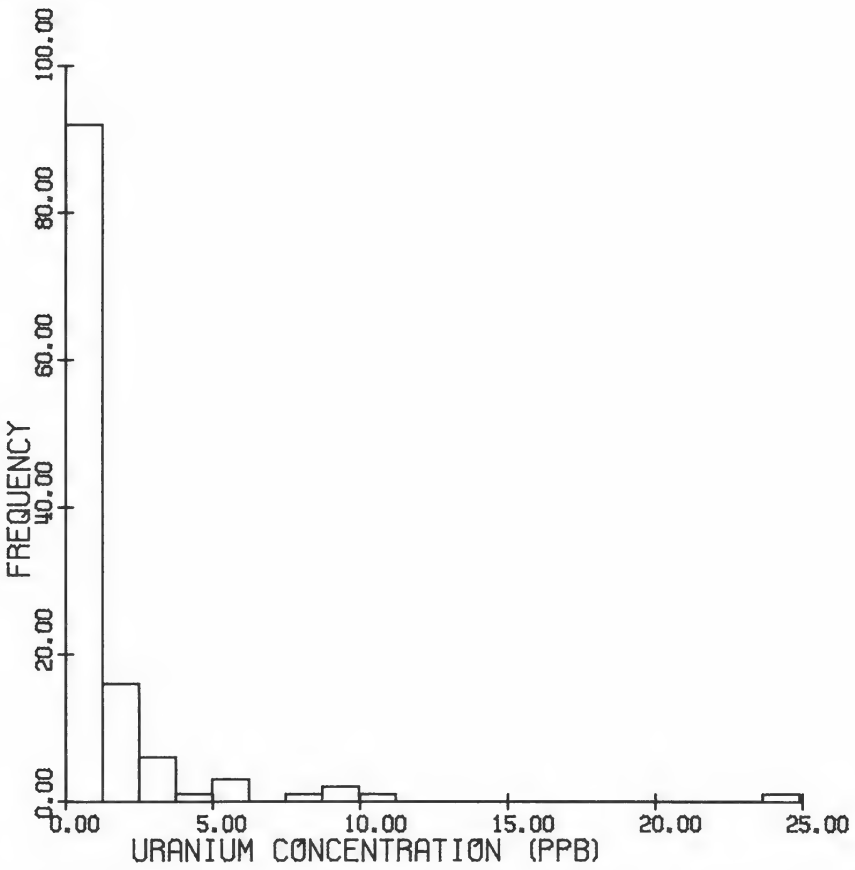


Figure 6. Distribution of uranium in parts-per-billion in the Pullman-Moscow basin. Most of the samples contain less than 4 ppb uranium. The height of the rectangular block is representative of the number of samples found within the given concentration range (modified from Ichimura, 1978).

Comparable ground water samples were collected from a 270-foot well (82.6 m) at the Midnite Mine which penetrates unweathered quartz monzonite of Cretaceous age adjacent to the ore body. Water from this well, which is near the discordant contact between the quartz monzonite and the host Togo formation, assayed 6.1 and 4.6 ppb, 125 and 125 micromhos at 25°C, and 7.0 and 7.0, uranium concentration, conductivity and pH, respectively. Based on this information and the arithmetic distribution of results from the Pullman-Moscow basin (Figure 6), any uranium content greater than 6.2 ppb is anomalous. This finding included about 6.8 percent of all samples. Additional work has shown that the data closely resemble a log-normal distribution characteristic of many trace element geochemical surveys (Ichimura, 1978).

In general, attempts to correlate conductivity, pH, and well depth with uranium concentration yielded linear correlation coefficients (r) of 0.20, 0.06, and 0.07, respectively. These values indicate no correlation, probably due to the varying environ-

ments of the shallow wells. However, data did show, generally, high conductivities for samples that had high uranium concentrations. This result is to be expected because uranium is generally correlated with high dissolved solids (salts). The correlation coefficient did not reveal this finding because of the scatter of conductivity data at lower uranium concentrations, especially in the shallower wells.

pH versus uranium concentration indicated that higher uranium concentrations are associated with near-neutral (pH = 7) samples. As expected, samples that are weakly alkaline display near-zero uranium concentration. The unexpected decrease in uranium concentration with increasing acidity appears to conflict with usual trends of increasing acidity and increasing solubility of uranium. Additional data provided by *in situ* Eh measurement and chemical assays of other ions in solution might better explain the reason for the above phenomenon.

Deeper, high capacity wells tapping basalt or interbedded aquifers almost always yield low uranium concentrations. This finding indicates possible ground water stratification where the deeper ground waters are devoid of oxygen and provide a possible fixation environment for uranium ions, as indicated by preserved organic matter found in some well cuttings.

It is important to note that a high uranium concentration (greater than 6.2 ppb) in ground water does not necessarily indicate a uranium deposit. These high uranium values reflect only ideal environmental conditions for uranium transport in solution at the location sampled. Reducing conditions common to ground water environments reduce the solubility of uranium greatly and result in low uranium assays regardless of uranium concentrations in aquifer matrix. Therefore, ground water sampling appears to be a less effective tool than surface-water sampling in geochemical exploration. Other tests, including drill core logging, natural gamma borehole logging, and radon gas measurement, may present additional needed information in the search for commercial uranium deposits.

## Conclusions

A refined nuclear track technique is an effective tool for uranium determination in ground water samples in geochemical exploration. The method is capable of detecting concentrations as low as 5.0 ppt and is far more sensitive than other commonly used analytical methods.

The technique has proven effective in locating clusters of high uranium concentration in ground waters from the east and southeast sections of the Pullman-Moscow basin on or near the basalt-granitic rock contact. These higher concentrations of uranium are probably due to local leaching of uranium from granitic rocks by oxidizing meteoric waters recharging the basin. Lower uranium concentrations were associated with deep, high-yield water wells located in the central and western sections of the basin. These results are probably indicative of the reducing nature of the deep, stratified ground water environment in the Pullman-Moscow basin.

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We wish to express our gratitude to F. H. Ruddy for his assistance and suggestions for improving the analytical method. Special thanks should go to F. F. Foit, Jr. for his critical review of the research project. We are also indebted to the staff of the Wash-

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# Variations of Grading in College Science Courses

**Abstract**

This study concludes that levels of achievement and the rigor of grading in pre-professional science courses vary significantly among some colleges and universities.

Many comparative studies of achievements in the high schools have been possible because the admissions procedures of most colleges and universities require the results of standardized tests (Astin, 1976; Stronck, 1979). A similar concern for predicting the probable achievements of students is found in the admission procedures to graduate schools. Unfortunately, our universities tend to use only the grades achieved in pre-professional courses to make any predictions about the possible success of students in advanced undergraduate courses. The published literature lacks studies comparing levels of achievement in the pre-professional courses. The use of only grades achieved in the pre-professional courses seems unwise when we recognize that between 1969 and 1976, A and B grades in American higher education rose from 35 percent to 59 percent of the total (Lamont, 1979).

The central question of this study is: Do grades achieved in advanced undergraduate courses at one nursing college correlate well with grades achieved in the prerequisite courses completed at a variety of colleges and universities? One nursing college in the Pacific Northwest annually admits 177 new students from approximately 230 applicants. This study considers three years of classes totaling 492 students admitted from six different classifications of institutions of higher education: A.) a local community college; B.) local small private four-year colleges; C.) distant community colleges; D.) distant universities; E.) a local state college; and F.) a large local university.

The prerequisite science courses for admission to this nursing college are the following: anatomy and physiology, chemistry, microbiology, and nutrition. The advanced science courses taught at the nursing college are pathophysiology, essentials of pharmacology, and advanced nursing. The subjects of this study were admitted into the nursing college with differences in their grades in the prerequisite science courses completed during their first two years of college. The differences among the six classifications of institutions of higher education were significant at the 0.04 level. The number of students in each classification with the grade point averages (based on a scale of 4.0) is given in Table 1. Note that the GPAs rank the classifications from highest to lowest in the sequence from A to F.

Also in Table 1 are the GPAs on the advanced science courses. These GPAs for

TABLE 1. Grade point averages in science courses by students in six classifications of institutions of higher education.

| Classification | Prerequisite | Rank | Nursing Courses | Rank | N |
|---|---|---|---|---|---|
| A. Local community college | 3.4734 | 1 | 2.5833 | 6 | 36 |
| B. Local private colleges | 3.3979 | 2 | 2.7597 | 5 | 43 |
| C. Distant community colleges | 3.3734 | 3 | 2.8627 | 4 | 34 |
| D. Distant universities | 3.3231 | 4 | 2.9755 | 2 | 74 |
| E. Local state college | 3.3026 | 5 | 2.9645 | 3 | 122 |
| F. Local large university | 3.2517 | 6 | 3.1075 | 1 | 183 |

each classification of institution differed at the 0.001 level of significance. The sequence of ranking on the achievements in the advanced science is almost the reverse of that for the GPAs on the prerequisite science courses (P equals –0.0429). This very strong negative correlation suggests that the grades in prerequisite courses should be interpreted according to the classification of the institution awarding the grade. For example, students in classification A tend to fall by almost 0.9 GPA from prerequisite courses to advanced science courses. On the other hand, students in classification F had a decline of less than 0.15 GPA. These data suggest that students in the last classification will probably have a negligible change in grade between prerequisite courses and advanced science courses. Nevertheless, the decline of almost a full point on the GPA among students of the first classification suggests the grading on the prerequisite courses was much less rigorous in this college than at the large local university.

TABLE 2. Grade point averages in all courses by students in six classifications of institutions of higher education.

| Classification | Prerequisite | Rank | Nursing Courses | Rank | N |
|---|---|---|---|---|---|
| A. Local community college | 3.3919 | 2 | 2.7700 | 6 | 36 |
| B. Local private colleges | 3.4381 | 1 | 2.8275 | 5 | 43 |
| C. Distant community colleges | 3.2651 | 5 | 3.1400 | 3 | 34 |
| D. Distant universities | 3.2101 | 6 | 3.1847 | 2 | 74 |
| E. Local state college | 3.3025 | 4 | 3.0180 | 4 | 122 |
| F. Local large university | 3.3266 | 3 | 3.1923 | 1 | 183 |

Table 2 provides the cumulative GPAs of the students before their admission to the nursing college. The ranking of these average GPAs on all courses before admission does not follow the simple pattern from A to F, i.e., from the local community college to the local large university. The most notable exception is that students coming from distant institutions (usually at least 150 miles away) had the lowest cumulative GPAs among those who were admitted. Nevertheless, the grades achieved by all students at the nursing college tended to resemble strongly the pattern on the three advanced science courses. The only strong exception here is the achievement of students from the local state college; their ranking remained unchanged. The correlation again was negative (P equals –0.600). The drop in GPAs between the cumulative GPA before admission and that achieved at the nursing college ranged from a maximum of 0.622 GPA in classification A to only 0.026 in classification D.

By contrasting the grading in advanced science courses at the nursing college (Table 1) with that of all courses at the same nursing college (Table 2), it is evident that

the grading in the advanced science courses is consistently more rigorous. On the other hand, no such trend is recognized when the prerequisite science courses are contrasted with the cumulative GPAs awarded before admission. The data of this study seem to indicate that the pre-professional science courses may provide grades similar to those from other introductory courses.

The most obvious conclusion from this study is that the levels of achievement and the rigor of grading in pre-professional science courses vary significantly among some colleges and universities. Although grades in prerequisite courses are generally good predictors of achievement in advanced courses, the type of institution awarding the grade is an important variable. According to Lamont (1979), those institutions which are most concerned about falling enrollments will tend to award credit for insufficient academic work and to tolerate continued grade inflation. Ashworth (1979) advocates the removal of those federal directives which encourage lower standards in institutions of higher education. Perhaps greater uniformity in the meaning of grades can be encouraged through providing faculty with comparative data on the achievements of their students in more advanced courses.

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# Successional Development in *Abies grandis* (Dougl.) Forbes Forests in the Swan Valley, Western Montana

## Abstract

*Abies grandis* is abundant and potentially climax over a major part of the Swan Valley in western Montana. This area is among the easternmost extensions of wet, low elevation forests related to the Pacific maritime climatic influence. Species coverage and site parameters were ascertained on 56 natural stands representing a wide range of site conditions and stand ages. The stand data were analyzed using polar ordination techniques.

Site moisture status and successional development are the most important factors determining species composition among the *Abies grandis* forests studied. The natural landscape in the Swan Valley is composed of a mosaic of various-aged stands. Few, if any, stands have reached climax status due to the repeated occurrence of fire. After intense fires, *Larix occidentalis* and *Pinus contorta* become established. When stands over 150 years old burn, *Larix occidentalis* tends to predominate in the regeneration; if the stands are younger, *Pinus contorta* tends to be favored. *Pseudotsuga menziesii* and *Pinus monticola* establish best during the first years of stand development and form an important component of many old stands. *Abies grandis* typically forms a layer below the *Larix occidentalis* or *Pinus contorta* canopy. Tree compositional changes along synthesized developmental pathways and understory alterations are discussed. This forest vegetation complex as a whole appears to have been stable under natural conditions; but on any given site, a wide range of communities occurred over time as wildfires repeatedly recycled the vegetation through a variety of developmental sequences.

## Introduction

The lower mountain slopes and intermountain valleys in parts of northwestern Montana (Fig. 1) support mesic, coniferous forests similar to those found in northern Idaho and eastern Washington. *Abies grandis*, *Pinus monticola*, *Thuja plicata*, and *Tsuga heterophylla* are conspicuous components of these forests. Eastward from northern Idaho across northwestern Montana, the distribution of these tree species becomes more discontinuous, with all of them reaching their range limits near the continental divide. Various problems associated with the origins and long term maintenance of these tree species in the northern Rocky Mountains have been the subject of recent interpretations and discussions by Daubenmire (1975).

The occurrence of mesic, low elevation forests in northwestern Montana is dependent upon the eastward penetration of moist Pacific air masses (Habeck, 1968). Glacier National Park contains stands dominated by *Thuja plicata* and *Tsuga heterophylla*; *Abies grandis* is only poorly represented. Southward from Glacier Park, however, the abundance of *Abies grandis* increases as *Thuja plicata* and *Tsuga heterophylla*

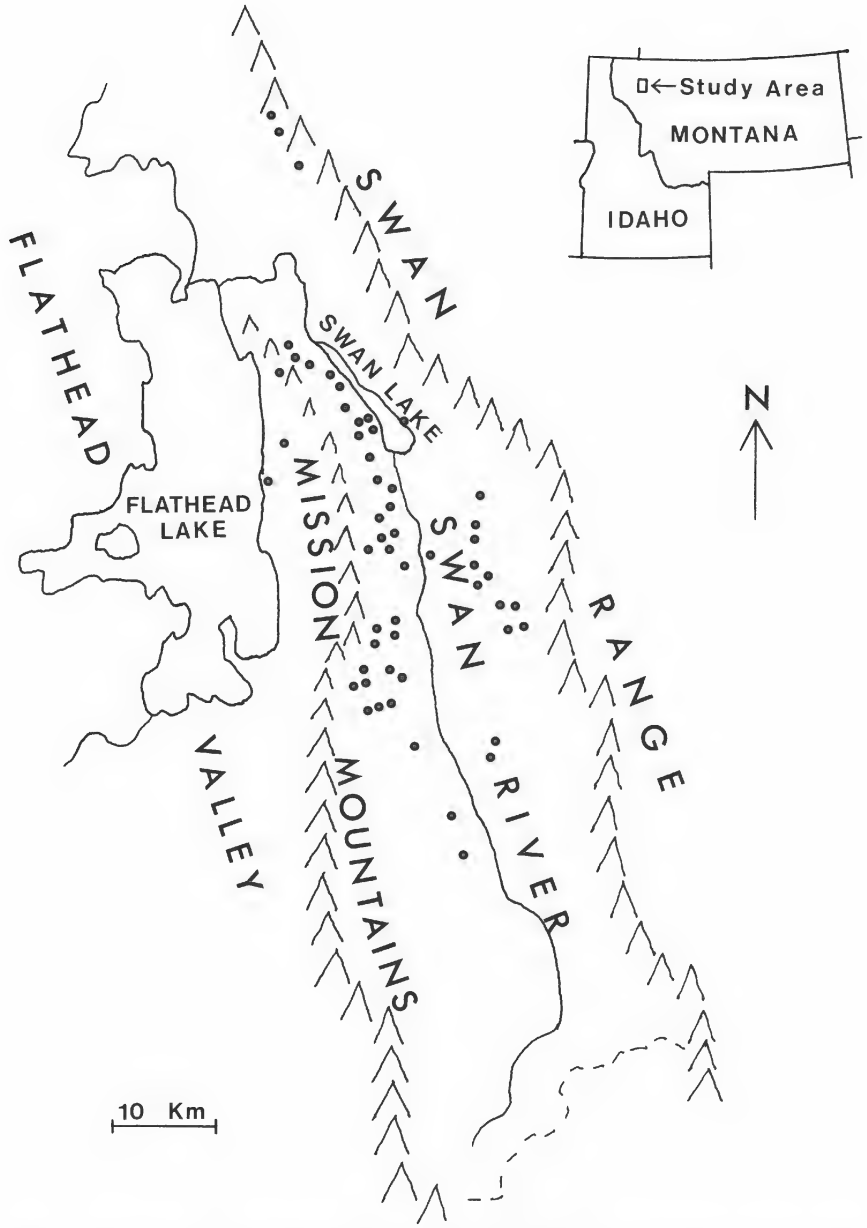


Figure 1. Map of the Swan Valley showing the general location and prominent features of the study area. The Swan Valley rises southward from 960 m at Swan Lake to about 1300 m at the southern end (dashed line). The Swan Range varies in elevation between 2000 m and 2800 m. The Mission Mountains begin near the north end of Flathead Lake and rise steadily southward, reaching 3000 m adjacent to the southern end of the Swan Valley. Dots represent stand locations.

diminish. Within the northern Swan Valley (Fig. 1), *Abies grandis* is a major forest dominant.

The major objectives of this paper are 1) to provide a descriptive interpretation of the compositional features of the *Abies grandis* containing forests occurring in the Swan Valley in northwestern Montana; and 2) to synthesize a description of post-disturbance successional recovery in this forest type. The latter is made through an analysis of a series of *Abies grandis* communities, collectively representing an array of past disturbances. Successional analysis conducted in this manner might be criticized on the basis that forest community re-establishment following disturbances is highly variable from site to site, and the severity of the disturbance treatments in different stands will also be variable (Drury and Nisbet, 1973; Lyon and Stickney, 1976). In spite of these apparent drawbacks, an effort is made in this report to construct a generalized model of successional development in the Swan Valley area.

The forests of the Swan Valley have received very little study in the past. Ayers (1900) examined forest conditions on the Flathead Forest Reserve; at the same approximate time, Whitford (1905) studied forests at the north end of the Swan Valley. Subsequent to these early investigations, no published reports have appeared dealing specifically with the phytosociology or successional relations of Swan Valley forests. Pfister *et al.* (1977) developed a habitat type classification for Montana forests. The forests considered in this paper fall within their *Abies grandis/Clintonia uniflora* habitat type, and to a lesser extent within their *Thuja plicata/Clintonia uniflora* habitat type.

**Study Area**

Swan Valley is located east of Flathead Lake, south of Glacier National Park, and west of the Bob Marshall Wilderness at latitude 47° north and longitude 114° west (Fig. 1). The valley, which is about 75 km in length and about 15 km in width, occupies most of the trench between the Mission Mountains to the west and the Swan Range to the east. The Mission Mountains are low (1000 m) at the north end of the Swan Valley, but increase to an elevation of 3000 m at the southern end of the valley. The steep scarp face of the Swan Range rises to a crest varying between 2000 and 2850 m elevation along the Swan Valley. The northward flowing Swan River passes across the broad, gently sloping valley, and through Swan Lake (935 m); at the north end, the river goes on to flow into Flathead Lake. The mountain masses are dissected by numerous east-west trending valleys cut by tributary streams of the Swan River.

The entire area is underlain by sedimentary rocks of the Belt Series (Johns, 1970). The bedrock is mostly argillite and limestone, with limestone predominating on the Mission Mountain side and argillite on the Swan Range side. During the Pleistocene, the entire area was glaciated by a combination of local mountain glaciers and cordilleran ice, which left a deep layer of till on the valley bottom and thinner layers on most mountain slopes. The soils show poor profile development. A prominent, reddish volcanic ash layer between 15 and 25 cm thick caps the soil on most sites. Below this ash layer occurs rocky to very rocky till except for a few locations with alluvial or residual material. An ash-gray $A_2$ less than 1 cm thick lies immediately below the duff layer on many sites.

The Swan Valley is affected by maritime air masses that yield heavy precipitation

upon intercepting the major mountain ranges east of the Flathead Valley. Swan Lake (935 m) at the north end of the valley receives 760 mm precipitation annually with peak amounts during winter and spring (Table 1). About one-third of the total falls from May through September. Swan Lake has an average July temperature of 16.9°C and January temperature of –5.1°C. Although very cold arctic air masses occasionally penetrate the area in winter, moist Pacific air masses predominate.

TABLE 1. Average precipitation and temperature values recorded at Swan Lake (960 m elevation; 21 yrs of record).

| | J | F | M | A | M | J | J | A | S | O | N | D | Yearly |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Precipitation (mm) | 106 | 66 | 54 | 42 | 51 | 80 | 31 | 45 | 48 | 62 | 85 | 87 | 756 |
| Temperature (°C) | -5.1 | -1.8 | 0.7 | 4.9 | 10.1 | 13.8 | 16.9 | 16.4 | 11.6 | 6.2 | 0.4 | -4.2 | 5.8 |

### Fire History

The Swan Valley is covered by a mosaic of stands of varying age and composition. Fire has been a major factor responsible for this variation. The earliest individuals to describe the vegetation of the Swan Valley were impressed with the importance of fire (Ayers, 1900; Whitford, 1905). They commented on the extensive impact of fire, the variable intensity of fires, and the vast amount of terrain supporting brush and tree reproduction as a result of past burns.

*Abies grandis* forests are characterized by high productivity which leads to rapid fuel accumulation, even though decomposition is rapid for Montana forests (Habeck and Mutch, 1973). During most summers, the occurrence of frequent rain makes intense fires unlikely; but in some years, dry summers set the stage for large crown fires. Most stands were initiated on large burns.

Judging from the area covered by stands of different ages, an average frequency of replacement burns of between 100 and 200 years was characteristic over most of the study area. Stands over 300 years old do occur, and repeat burns less than 20 years apart have also occurred. In some forests initiated by replacement burns, ground fires have occurred after stand establishment, with variable effects on the overstory. Very wet sites such as stream bottoms and lower north slopes often experience partial burns when located within the perimeter of large replacement burns.

During the first third of this century, intense fires burned a large part of the Swan Valley. Since 1940, fire suppression has been increasingly effective in confining most fires to several hectares or less in size within the *Abies grandis* forest areas. Modern fire suppression has led to a reduction in the number of young pioneer stands; this effect has caused a significant gap in the successional sequence.

### Methods

During the summers of 1975 and 1976, 56 *Abies grandis* forest communities were quantitatively sampled. These stands were chosen to represent a wide range of variation in stand ages and site characteristics. Only stands showing no significant signs of human disturbance were included. In each stand, a circular 375 $m^2$ plot was established in a location believed to be typical of the entire stand (Pfister *et al.*, 1977).

Within this plot, canopy coverage values were assigned to each vascular species, following the procedures described by Pfister *et al.* (1977). All trees in each plot were tallied by 5 cm diameter size classes. Xylem-ring counts were made on from 3 to 10 trees per stand in order to establish stand ages and ages of tree reproduction. Site parameters such as topographic position and soil characteristics were recorded for all stands.

The 56 stand samples were subjected to a multidimensional polar ordination analysis following the basic procedures of Bray and Curtis (1957), except that end stands were subjectively chosen. Additional analysis employed direct gradient techniques as described by Whittaker (1956, 1967). Results from the direct gradient analysis were compared with the polar ordination to help determine vegetation-environment relationship.

#### Results and Discussion

The ordination (Fig. 2) indicated that two major gradients are correlated with the

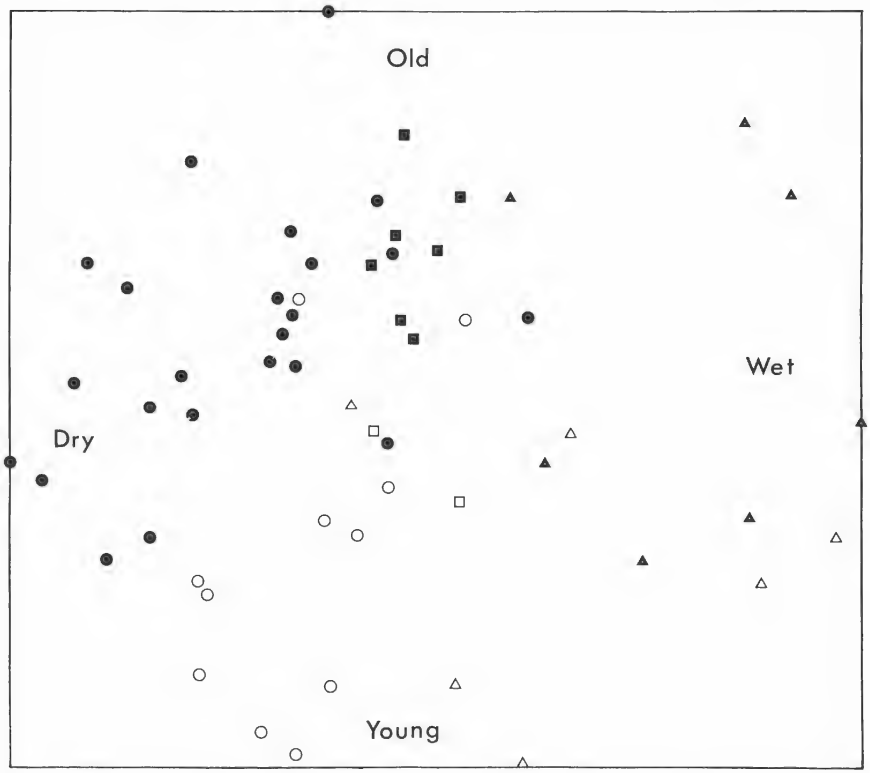


Figure 2. Polar ordination of the 56 stands made by using the data for all species. The end stands on the x-axis are 68 percent and on the y-axis 59 percent dissimilar. Squares represent stands with over 5 percent coverage of *Taxus brevifolia*, triangles greater than 5 percent coverage of *Thuja plicata*, and circles all other stands. Solid symbols represent stands with less than 5 percent coverage of *Pinus contorta*.

compositional organization of the *Abies grandis* communities in the Swan Valley: 1) a site moisture gradient; and 2) a temporal gradient which corresponds to successional development.

The ordination suggests that elevation does not correlate well with the compositional variation among the 56 stands sampled. *Abies grandis* communities occur from stream level elevations (about 1000 m) up to about 1600 m. *Thuja plicata* has an upper elevational limit very similar to that of *Abies grandis*, but the other major conifer species and many of the associated understory species extend from the Swan Valley floor to well above the upper limits observed for *Abies grandis.* The forests immediately above this limit are compositionally similar to those below, except that *Abies grandis* is replaced by *Abies lasiocarpa.* On the lowest parts of the valley floor, *Abies grandis* is often absent, although the forests in other respects are very similar to those containing the species. Temperature inversions are known to decrease the frost-free season on the floors of mountain valleys (Daubenmire, 1959), and this factor may be the central one involved here.

*Abies grandis* occurs on nearly all aspects in the northern Swan Valley; it is absent only on steep south-facing slopes with shallow soils. Further southward, *Abies grandis* becomes gradually restricted to moist sites so that in the southern Swan Valley the species is much less common. *Thuja plicata* is a major forest component on sites such as lower north slopes and streamsides. On such sites, *Abies grandis* and *Thuja plicata* occur together in variable proportions. *Thuja plicata* can occur as a significant forest component on approximately the wetter one-third of the sites which support *Abies grandis. Tsuga heterophylla* is rare in the Swan Valley.

In the Swan Valley, the major seral species, *Larix occidentalis, Pinus contorta*, and *Pseudotsuga menziesii*, span the entire range of moisture and temperature conditions tolerated by *Abies grandis* (Antos, 1977). They are capable of growing well on all the sites considered here, with their relative abundance determined more by stand history than site characteristics. *Pinus monticola* often grows on all *Abies grandis* sites except the driest; it comprises a high proportion of some stands.

Some understory species occupy the entire range of moisture conditions supporting *Abies grandis*; others are confined to either the wet or dry sites. The driest *Abies grandis* sites support many understory species which occur on *Pseudotsuga menziesii* climax sites (Antos, 1977). Groves of large *Thuja plicata* with a luxuriant herbaceous layer and some *Abies grandis* occur on a few streamside sites.

The coverage achieved by the herbaceous layer species is related to overstory density (Antos, 1977; McCune, 1979). Open canopied stands on both the wet and dry sites support continuous herb layers, but dense stands have few plants beneath the canopy. The low shrub layer is not well developed except in stands with a thin canopy. In most stands, there is an intermittent tall shrub layer 4-7 m tall composed of *Acer glabrum.* A layer of *Taxus brevifolia* with a coverage of 25-75 percent is characteristic of wetter *Abies grandis* stands which do not contain much *Thuja plicata.*

### Post-Fire Successional Patterns

The successional recovery patterns following high intensity "replacement" fires on average *Abies grandis* sites will be described and discussed first. These sites all correspond to the *Abies grandis/Clintonia uniflora* habita type of Pfister *et al.* (1977).

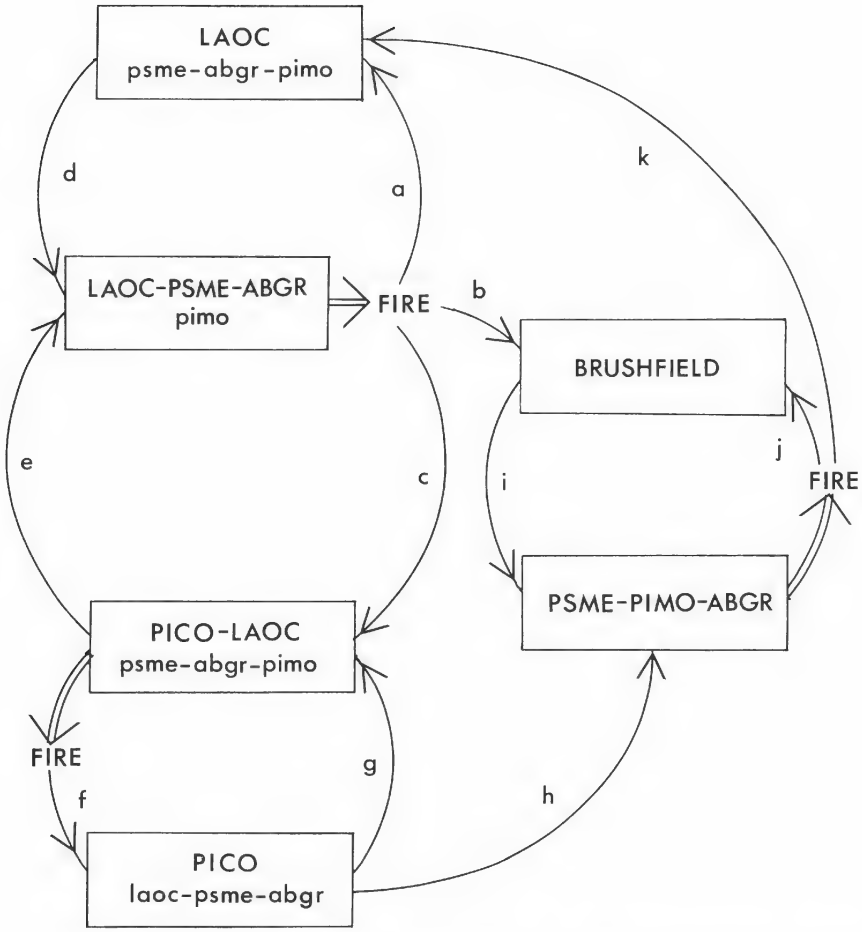


Figure 3. Patterns of forest community dynamics within the Swan Valley. (A. Pico* seed source absent; B. Laoc and Pico establishment fail; C. Pico seed source present; D. Psme and Abgr increase with time; E. Pico dies out of the stand; F. burned stand young enough that Laoc does not survive fire so Pico increases; G. Pico decreases; H. Pico dies out and no Laoc in the stand; I. Slow brushfield invasion; J. no Laoc seed source present; and K. Laoc seed source present.)

*Laoc = *Larix occidentalis*, Psme = *Pseudotsuga menziesii*, Abgr = *Abies grandis*, Pimo = *Pinus monticola*, Pico = *Pinus contorta*; capitals = major species, lower case = minor species.

Figure 3 presents generalized successional pathways that are hypothesized to be significant in Swan Valley *Abies grandis* forests following replacement burns. This model was derived from a variety of sources, including ordination patterns, stand data, and extensive field observations. It is used here to facilitate the discussion of successional development patterns, and the reader should realize that it is tentative and will no doubt need revision as more information is obtained about these forest ecosystems.

Most old-growth forests (greater than 150 years old) on Swan Valley *Abies grandis* sites have an overstory 35-40 m tall, composed of *Larix occidentalis* and *Pseudotsuga menziesii* with occasional *Pinus monticola.* Beneath the overstory occur numerous small diameter *Abies grandis*, interspersed with larger sized *Abies grandis* which on occasion reach to the upper canopy level. *Abies lasiocarpa* and *Picea engelmannii* (or *Picea engelmannii* X *P. glauca* [Habeck and Weaver, 1969]) occur as scattered individuals, but *Pinus contorta* is often absent. When a fire removes most or all of the canopy in such a stand, one of three major routes of development appears to be followed.

If *Pinus contorta* seed is scarce or unavailable while *Larix occidentalis* seed trees are present in the vicinity, a stand with a *Larix*-dominated overstory will develop (Fig. 3, path A). *Larix occidentalis* is the most fire resistant tree in the Swan Valley (Flint, 1925; Schmidt *et al.*, 1976), and a few mature individuals survive most wildfires. Following large forest fires of the early 1900s, well-stocked *Larix occidentalis* stands developed from a very few surviving seed trees. *Larix occidentalis* seedlings establish well on burned-over surfaces where mineral soil is exposed, but do not compete successfully in dense shrub or forb cover, or become established on a thick duff layer (Fowells, 1965; Schmidt *et al.*, 1976; Shearer, 1975). Consequently, most young *Larix* become established within the first few years following a fire. *Pseudotsuga menziesii* establishment and early growth is slower (Fowells, 1965), but this species is sufficiently shade tolerant to persist and may eventually reach the upper canopy layer. *Abies grandis* establishes more slowly and initial growth is slow; therefore, most individuals become suppressed. If canopy openings develop when the stand is young, *Abies grandis* exhibits rapid growth and can achieve a position in the main canopy. Initial growth of *Pinus monticola* is rather slow (Fowells, 1965). As a result, *Pinus monticola* is frequently overtopped by *Larix occidentalis.* Very rapid growth occurs if overhead light is present; thus, when a gap develops in the canopy, *Pinus monticola* individuals can achieve dominant positions (Antos, 1977). As the young stand increases in age, the proportion of *Pseudotsuga menziesii* in the canopy layer often increases while the characteristic *Abies grandis* understory develops to yield an old stand similar to the one which burned (Fig. 3, path D).

In those cases where the burned stand still supported some *Pinus contorta*, the new pioneer forest will have an overstory composed of a mixture of *Pinus contorta* and *Larix occidentalis* (Fig. 3, path C). *Pinus contorta* dies out 120-160 years following burning. As a consequence, there are no seed sources in older stands. Only 40 percent of the sampled stands over 150 years of age ($n = 21$) have any *Pinus contorta* remaining. Stands dominated by various proportions of *Pinus contorta* and *Larix occidentalis* are abundant on the large burns originating from the early 1900s. With the demise of *Pinus contorta, Pseudotsuga menziesii* often fills the canopy gaps and produces a mature stand similar to the one which burned (Fig. 3, path E).

Mixed *Pinus contorta-Larix occidentalis* stands that burn before much of the *Pinus contorta* has died out (120 years old) are replaced by stands with a higher proportion of *Pinus contorta* in the canopy than in the pre-burn stand (Fig. 3, path F). In immature forests, *Larix occidentalis* still has thin bark and thus cannot survive most fires (Schmidt *et al.*, 1976), while the *Pinus contorta* closed cone seed source is abundant. Concomitant with the break-up of the *Pinus contorta* canopy, a heavy fuel bed is created, which increases the potential for intense fires (Brown, 1975). Stands

strongly dominated by *Pinus contorta* are thus formed. Stands of this type have few individuals of other tree species present if located in the center of very large burns, but if the stands occur near the edges of burns, numerous *Abies grandis* and *Pseudotsuga menziesii* are present below the *Pinus contorta* canopy.

Since *Larix occidentalis* grows much larger than *Pinus contorta*, stands containing as little as 10 percent *Larix* can eventually develop a *Larix*-dominated overstory (Fig. 3, paths E and G). Mature stands formed in this way often resemble stands formed where *Larix occidentalis* was the major pioneer tree species except for a larger proportion of *Pseudotsuga menziesii* and a lower proportion of *Larix occidentalis* in the canopy layer.

Stands with a pure *Pinus contorta* overstory undergo a drastic change when this layer breaks up (Fig. 3, path H). The resulting new canopy will often be dominated by *Pseudotsuga menziesii* and *Abies grandis*, with lesser amounts of *Pinus monticola* and *Picea*. This path does not seem to have been followed often in the past due to the high fire danger during the break-up of old-aged *Pinus contorta* stands. Whenever *Pinus contorta* stands burn, they regenerate themselves. Repeated fires at intervals of less than 100 to 150 years favor *Pinus contorta*, while a fire interval of over 200 years can eliminate this species from the forest. Both conditions and all gradations in between are present in the Swan Valley. Some drainages support mostly old stands with almost no *Pinus contorta* present; others contain extensive young stands dominated by this species as the result of short interval repeat burns.

In several tributary drainages, mature forests dominated by *Pseudotsuga menziesii, Pinus monticola*, and *Abies grandis* with some *Picea* occur. These forests might have developed through the break-up of *Pinus contorta* stands (Fig. 3, path H), or through brushfield invasion (Fig. 3, path I). Where *Pinus contorta* is absent and a fire intense enough to destroy the *Larix occidentalis* seed source occurs, a brushfield can develop. There are no extant examples of natural brushfields in the Swan Valley because of the long period of fire exclusion and the fact that none of the burns dating from the early 1900s followed this route; but several lines of evidence indicate that brushfields could have occurred in the past. Brushfields are common in other areas due to wildfires in similar forest types (Mueggler, 1965). Brushfields have formed on some clearcuts. The invasion of a brushfield community would yield the composition noted for these old *Pseudotsuga menziesii, Pinus monticola, Abies grandis*, and *Picea* dominated stands. These species can invade a brushfield, although often very slowly, but *Larix occidentalis* and *Pinus contorta* cannot (Antos, 1977). The burning of stands of this sort can lead to brushfield formation again and the cyclic redevelopment of the same type of stand (Fig. 3, paths I and J). If a *Larix occidentalis* seed source is fortuitously present in nearby stands, a stand dominated by this species can also develop (Fig. 3, path K).

Successional patterns on the driest sites on the *Abies grandis/Clintonia uniflora* habitat type are similar to those just described except for the great importance of *Pseudotsuga menziesii* and absence of *Pinus monticola*.

### Succession on Wet Sites

Successional patterns on the wettest sites within the *Abies grandis/Clintonia uniflora* habitat type and on the *Thuja plicata/Clintonia uniflora* habitat type are similar in

many respects to those already described, but there are some important differences related to the presence of *Thuja plicata.* This species forms a layer with a coverage of greater than 50 percent beneath an overstory of *Larix occidentalis* and/or *Pinus contorta* in many stands. On other sites which are just as moist, judging from topographic position and understory composition, *Thuja plicata* is rare or absent and *Abies grandis* is the prevalent shade tolerant species. The factors determining the proportions of these two shade tolerant species which occur in a stand are linked to the early stages of stand development.

After a fire, the duff layer is thinned or removed, and the amount of light reaching the ground greatly increased. Also, transpirational water loss and canopy interception are diminished, which leads to increased soil water except in the surface layer where evaporation is effective (Daubenmire, 1959; Schmidt *et al.*, 1976; Shearer, 1975). Such conditions are favorable for the establishment of both pioneer and shade tolerant tree species (Fowells, 1965; Haig *et al.*, 1941). Extensive observations of tree seedlings during this study indicate that *Thuja plicata* only establishes in significant numbers on damp mineral soils such as north slopes, upon which soil surface evaporation is slow. Some shade is beneficial in retarding surface evaporation, but dense vegetation appears to prevent *Thuja plicata* seedling establishment.

As stand development proceeds, *Thuja plicata* seedling establishment decreases. Most *Thuja* seedlings become established during the first 10-20 years after a fire. *Thuja plicata* reproduction can be very dense; 17,000 stems per hectare were counted in one 40-year-old stand. *Thuja plicata* often subsequently increases through vegetative layering; the important point, however, is that if the species does not enter during the first years of stand development, it probably will not do so later on. Excavation of root systems of small (20-40 cm tall) *Abies grandis* and *Thuja plicata* growing next to each other indicates that the latter have shallower root penetration. This finding is consistent with observations by Haig *et al.* (1941) in northern Idaho. At least in part because of deeper root penetration, *Abies grandis* can continue establishing in a stand long after *Thuja plicata* establishment becomes difficult (Antos, 1977).

In the generalized successional diagram (Fig. 3), *Thuja plicata* can be added in most places in which *Abies grandis* occurs. After high intensity fires, *Thuja plicata* is often a more aggressive invader than *Abies grandis.* When seed is limited, such as in the centers of large burns, both *Thuja plicata* and *Abies grandis* will gradually invade the site because the typical semi-open overstory of *Pinus contorta* does not completely inhibit seedling establishment. The establishment of shade tolerant species can require many years on such sites.

The major successional path that is not open to *Thuja plicata* involves brushfield invasion. Some very wet sites within the Swan Valley support old-growth forests dominated by *Pseudotsuga menziesii, Pinus monticola, Abies grandis*, and *Picea.* We believe that these sites can probably support *Thuja plicata* but do not because of the following process. Following intense wildfire, pioneer species such as *Larix occidentalis* and *Pinus contorta* failed to establish due to either inadequate seed source, unfavorable weather, or some other reason. A brushfield thus developed. Only tree species that are at least somewhat shade tolerant when young, as well as capable of establishing in the soil under or between the shrubs, could invade the site. Gradual invasion of brushfield communities by such species would yield the appropriate com-

position for the old-growth stands present today (Antos, 1977). *Thuja plicata* is shade tolerant, but less able to establish under the shrubs; moreover, it often cannot enter an established stand, as we have indicated.

### Understory Changes

Since there are no recent natural burns in the study area, direct examinations of the earliest stages of vegetation recovery are not possible. Observations in available examples of logged sites subject to prescription burning, however, indicate that major changes in understory composition coincide with tree canopy closure. At this time or shortly thereafter, shade intolerant pioneer species are eliminated from the stand. Subsequent to canopy closure, most changes in the understory layer involve alterations in species abundance or proportions but not species loss or replacement. Table 2 summarizes presence and coverage data for a series of stands 30-90 years old and others greater than 150 years old. Most ground layer species show little change in their occurrences between younger and older stands. The 30-90 year old stands have all achieved canopy closure and thus provide understory microclimatic conditions more similar to mature stands than stands under 20 years of age.

TABLE 2. Representative species changes between immature stands (less than 90 yrs old) and old-growth stands (greater than 150 yrs old) which have resulted from replacement burns on **Abies grandis** sites in the Swan Valley. Percent presence is shown to the left of the slash and percent coverage (based on all stands in each category; t = less than 1 percent) is shown to the right of the slash. Nomenclature follows Hitchcock and Cronquist (1973). (* = change in coverage significant at the 0.05 level.)

| | Immature Stands (n = 9) | Old Stands (n = 15) | |
|---|---|---|---|
| **Abies grandis** | 78/25 | 100/58 | * |
| **Abies lasiocarpa** | 33/t | 60/3 | * |
| **Acer glabrum** | 100/12 | 100/19 | |
| **Adenocaulon bicolor** | 56/2 | 100/5 | * |
| **Amelanchier alnifolia** | 78/3 | 60/1 | |
| **Arnica latifolia** | 33/13 | 47/3 | |
| **Berberis repens** | 78/3 | 80/t | |
| **Betula papyrifera** | 56/2 | 33/1 | |
| **Bromus vulgaris** | 33/t | 80/t | * |
| **Calamagrostis rubescens** | 67/2 | 33/1 | |
| **Carex concinnoides** | 78/t | 60/t | |
| **Chimaphila umbellata** | 100/5 | 93/2 | |
| **Clintonia uniflora** | 78/2 | 100/5 | |
| **Corallorhiza maculata** | 33/t | 33/t | |
| **Disporum hookeri** | 67/4 | 73/4 | |
| **Festuca occidentalis** | 11/t | 40/t | |
| **Fragaria vesca** | 67/t | 7/t | * |
| **Galium triflorum** | 11/t | 33/t | |
| **Goodyera oblongifolia** | 89/t | 100/t | |
| **Gymnocarpium dryopteris** | 0/0 | 20/t | |
| **Hieracium albiflorum** | 78/t | 53/t | |
| **Holodiscus discolor** | 33/t | 7/t | |
| **Larix occidentalis** | 89/13 | 100/19 | |
| **Linnaea borealis** | 56/t | 80/2 | |
| **Listera caurina** | 44/t | 47/t | |
| **Lonicera ciliosa** | 22/t | 33/1 | |
| **Lonicera utahensis** | 33/t | 67/t | |
| **Melica subulata** | 44/t | 20/1 | |
| **Menziesia ferruginea** | 11/t | 53/4 | |
| **Osmorhiza chilensis** | 33/t | 73/t | |
| **Pachistima myrsinites** | 89/7 | 100/t | * |

| | | | |
|---|---|---|---|
| **Pedicularis racemosa** | 33/t | 13/1 | |
| **Picea sp.** | 56/2 | 80/6 | |
| **Pinus contorta** | 89/52 | 33/4 | * |
| **Pinus monticola** | 44/2 | 87/20 | * |
| **Pseudotsuga menziesii** | 89/29 | 100/30 | |
| **Pteridium aquilinum** | 56/4 | 20/t | |
| **Pyrola asarifolia** | 22/t | 67/t | * |
| **Pyrola chlorantha** | 22/t | 67/t | |
| **Pyrola picta** | 11/t | 20/t | |
| **Pyrola secunda** | 78/t | 73/t | |
| **Ribes viscosissimum** | 44/t | 0/0 | * |
| **Rosa gymnocarpa** | 78/6 | 100/4 | |
| **Rubus parviflorus** | 89/3 | 40/t | * |
| **Salix scouleriana** | 89/9 | 0/0 | * |
| **Shepherdia canadensis** | 33/t | 0/0 | * |
| **Smilacina racemosa** | 33/t | 20/t | |
| **Smilacina stellata** | 78/t | 87/2 | |
| **Sorbus scopulina** | 22/t | 20/t | |
| **Spiraea betulifolia** | 89/3 | 93/3 | |
| **Symphoricarpus albus** | 67/2 | 40/t | |
| **Taxus brevifolia** | 22/2 | 47/15 | |
| **Thalictrum occidentale** | 44/t | 47/1 | |
| **Thuja plicata** | 44/t | 33/t | |
| **Tiarella trifoliata** | 33/t | 47/1 | |
| **Vaccinium globulare** | 78/t | 93/9 | * |
| **Viola orbiculata** | 67/t | 80/t | |
| **Xerophyllum tenax** | 100/9 | 100/14 | |

Following canopy closure, some stands enter a period when shrubs and herbs are reduced to and maintained at very low coverage (the "stagnation stage" of Daubenmire and Daubenmire, 1968). This stagnation phase occurs only if a layer of shade tolerant tree species is present, since an overstory composed primarily of *Larix occidentalis* or *Pinus contorta* is not sufficient to induce a sparse understory. This depauperate condition can persist for a long time: it was observed in stands ranging from 35 to over 200 years in age. As stands grow older, sporadic tree mortality leads to gaps of various sizes within which the herb and shrub layers can develop coverages near 100 percent. Stands with many large openings are often floristically rich because they have the largest array of microsites.

Low intensity fires occur at times, especially on moist sites. In such cases, the upper organic soil layers are reduced in depth and the canopy partially removed, providing excellent establishment conditions for shade tolerant tree species. *Abies grandis* and/or *Thuja plicata* often form a layer approaching 100 percent coverage in such cases. These stands have the most depauperate herb and shrub layers of any observed. *Pseudotsuga menziesii* and *Pinus monticola* may also establish under such conditions, but *Larix occidentalis* and *Pinus contorta* rarely do (Antos, 1977).

### The Climax

A unit of vegetation can be considered to have reached a climax status when it attains a high degree of compositional stability. Very few stands in the Swan Valley give evidence of having reached this state. The concept of the climax can be useful, however, as long as it is realized that climax is not a state that is normally achieved among the Swan Valley *Abies grandis* forests, but merely a theoretical point upon which to focus trends which do occur in the vegetation. Over the whole study area and spanning the long course of time, this forest vegetation is a relatively stable composite; on any one site, however, fire induces a state of fluctuation in the ecosystem.

Any one site can be occupied by a myriad of variations ranging from fresh burns through a variety of successional stands to differing types of old forests.

As a stand develops, establishment of all tree species below the canopy, including *Abies grandis*, becomes difficult. With time, almost all tree species establishment becomes confined to openings. *Abies grandis* is most successful at this kind of establishment. In old-growth stands, there are often many small *Abies grandis* (1-4 m tall), a fact which gives the impression of abundant regeneration. But closer inspection reveals a distinct lack of newly established individuals except in openings. The cutting of hundreds of small *Abies grandis* during the course of this study showed that these trees are old. Suppressed *Abies grandis* from 1-4 m tall are rarely less than 40 years old and can be over 120 years in age with an average age of about 75 years. *Abies grandis* can survive under dense shade, but makes very slow growth, often 1 or 2 cm per year. In contrast, trees which attain overhead light at a young age can make rapid growth and reach a dominant position in the canopy.

On typical sites in the Swan Valley study area, *Abies grandis* dominates the reproduction and is clearly the indicated climax species. Only a few stands have escaped fire long enough for *Abies grandis* to have formed a major portion of the canopy layer. Since *Pseudotsuga menziesii* and *Pinus monticola* can establish in openings, there is no reason why these two species will not persist indefinitely as minor forest components. The same can be said for *Abies lasiocarpa* and *Picea.*

Sites capable of supporting *Thuja plicata* have a more complex post-fire developmental pattern. Not only do the initial years of stand development determine which pioneer species will be present; they also determine which shade tolerant species will predominate. Most tree reproduction eventually becomes confined to openings, and *Abies grandis* appears to be more successful than *Thuja plicata* at establishing in openings. In stands in which *Thuja plicata* is established, it will persist through vegetative means such as branch layering. There is no conspicuous tendency for either of these species to replace the other completely. Neither is an ideal climax species in the traditional sense since both are unable to establish well from seed under their own shade. There is no selective pressure for genotypes which can establish under a dense forest canopy because under natural conditions the forest burns before the trees originally present die. The wetter the site, the more likely that *Thuja plicata* will predominate due to this species aggressive seedling establishment on burns. Within this context, however, the relative proportions of *Thuja plicata* and *Abies grandis* in a stand are a function of conditions during the years of stand initiation and do not change much until the next fire occurs.

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# Canopy Cover and Phytomass Comparisons of Steep Slopes Planted to Cheatgrass[1]

**Abstract**

Steep north- and south-facing slopes on an artificially formed earth mound were seeded with cheatgrass in the autumn of 1971 and left unattended. In 1978, canopy cover and phytomass measurements were made on both slopes. The vegetative cover on the north-facing slope provided more canopy cover and more live phytomass than the south-facing slope. Live aboveground phytomass was measured at 830 $g/m^2$ on the north-facing slope and 163 $g/m^2$ on the south-facing slope.

The large amount of primary production on the north-facing slope is attributed to temperature-water relationships rather than to soil nutrient differences because the mound was composed of the same homogeneous mix of soil of common origin.

## Introduction

Plants that comprise native steppe communities provide a more or less continuous ground cover, but the amount of cover and its species composition vary greatly from place to place according to the rooting substrate and to variations in microclimate as influenced by major and minor topographic features of the land.

Sauer and Rickard (1979) examined species composition and canopy cover on natural north- and south-facing slopes. They found that steep north-facing slopes supported more species and more canopy cover than contrasting south-facing slopes, but the rooting substrates on the contrasting slopes were also markedly different, with the north-facing slopes having a rooting substrate more favorable to plant growth. In field investigations it is usually not possible to separate substrate variables and those variables caused by slope exposure in terms of plant growth.

Hinds (1975) examined energy and soil water relationships and was able to control the rooting substrate by raising plants in small weighing lysimeters filled with the same kind of soil and then exposing the lysimeters to the contrasting microclimates of north- and south-facing slopes. In this way, differences in plant productivity and phenology could be attributed to microclimatic rather than soil variables.

## Methods and Materials

An artificial earth mound 100 m long and about 2 m in height was constructed by scraping the surface soil of the surrounding ground into shape with a bulldozer. The long axis of the mound extended in an east-west direction forming steep (40°) north- and south-facing slopes. The slopes were seeded with cheatgrass by hand sowing in early autumn and left unattended (Hinds, 1974).

Canopy cover by species was determined twice during the growing season of

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1978 on 10 March and again on 17 April. One line, 25 m long, was located at mid-slope and parallel to the long axis of the mound on the north slope; another line was placed along the south slope. Canopy-cover was estimated visually on 50 plots placed systematically at ½ m intervals along each line (Daubenmire, 1959). The same lines were used in March and April.

Aboveground plant parts were harvested by hand picking all live plants within circular plots placed along but not on the line used for canopy cover estimates. Small plots 0.032 $m^2$ were used during the winter and early spring harvests, but 0.5 $m^2$ plots were used when plants were mature at the end of the growing season. Only five plots were harvested on each slope early in the growing season, but ten plots were harvested at the end of the growing season. Live plant material was separated from any dead plant material by hand sorting. The live material was air dried in the laboratory and weighed. Results are presented as grams dry weight per square meter. Dead plant material (litter) was hand picked from each plot harvested for aboveground phytomass, air dried, and weighed in the same way employed for live phytomass.

#### Results and Discussion

Only a few taxa grew on the earth mound. All were self-established following the initial seeding of cheatgrass. Cheatgrass, *Bromus tectorum*, and tumble mustard, *Sisymbrium altissimum*, were the most abundant species. Other taxa were Russian thistle, *Salsola kali*, spring draba, *Draba verna*, tansy mustard, *Descurainia pinnata*, willow herb, *Epilobium paniculatum*, bluebunch wheatgrass, *Agropyron spicatum*, Sandberg bluegrass, *Poa sandbergii*, Cusick bluegrass, *Poa cusickii*, hawks' beard, *Crepis atrabarba*, yellow salsify, *Tragopogon dubius*, fleabane, *Erigeron filifolius*, and big sagebrush, *Artemisia tridentata*. Plants provided more canopy cover on the north-facing slope than the south-facing slope (Table 1).

Phytomass harvests show the north-facing slope to be more productive from the initiation of growth in the fall to senescence in late spring (Fig. 1). The growing season was also longer on the north-facing slope. The poor showing of early fall plant growth in the south-facing slope is probably due to more intense solar radiation which results in evaporative loss of soil water.

The accumulation of dead plants (litter) was not clearly favored on one slope or the other (Table 2). The variation among samples taken from either slope was large, as indicated by the size of the standard error associated with the mean. Variation was probably induced by the heterogeneity of the litter mat on the slope due to a tendency of litter to accumulate in microdepressions. However, it is also possible that litter decomposition is faster on the north-facing slope due to a more favorable moisture regime.

Plant growth was initiated for the 1978 season with the onset of rains in the autumn of 1977. Growth was arrested during the cold winter months and resumed with the onset of warming temperatures and increasing day length in spring (Fig. 1). Plants matured on the south-facing slope in mid-April, but maturation and senescence on the north-facing slope was delayed until mid-May. At the termination of the growing season, the north-facing slope had produced 830 g of dry matter per $m^2$ compared to only 163 $g/m^2$ on the south-facing slope. Cheatgrass was the major contributor to productivity on the north-facing slope, but tumble mustard was almost

TABLE 1. Summary of canopy cover (percent) on steep slopes of an artificial earth mound in the spring of 1978.

| | North-facing slope | | South-facing slope | |
|---|---|---|---|---|
| | Mar 10 | Apr 17 | Mar 12 | Apr 17 |
| **Annual Grasses** | | | | |
| Cheatgrass[a] | 63 | 84 | 24 | 30 |
| **Annual Forbs** | | | | |
| Tumble mustard[a] | 12 | 26 | 22 | 65 |
| Tansy mustard | 1 | 1 | 1 | 1 |
| Willow herb | 0 | 1 | 0 | 0 |
| Spring draba[a] | 0 | 1 | 0 | 0 |
| Russian thistle[a]* | 0 | 0 | 0 | 1 |
| **Perennial Grasses** | | | | |
| Bluebunch wheatgrass | 1 | 1 | 0 | 0 |
| Sandberg bluegrass | 0 | 1 | 0 | 0 |
| Cusick bluegrass | 0 | 1 | 0 | 0 |
| **Perennial Forbs** | | | | |
| Hawks' beard | 0 | 1 | 0 | 0 |
| Fleabane | 0 | 0 | 0 | 1 |
| Yellow salsify[a] | 0 | 1 | 0 | 0 |
| **Shrubs** | | | | |
| Big Sagebrush* | 0 | 0 | 0 | 1 |
| Total Canopy Cover % | 77 | 118 | 47 | 99 |
| Total Taxa | 4 | 10 | 3 | 6 |

* = seedlings
[a] = naturalized immigrant

TABLE 2. Dead phytomass on north and south slopes of an artificial earth mound.

| Date | North $g/m^2 \pm SE$ | South $g/m^2 \pm SE$ |
|---|---|---|
| Dec 15 | 449 ± 80 | 308 ± 52 |
| Feb 10 | 443 ± 84 | 357 ± 50 |
| Feb 22 | 244 ± 77 | 335 ± 84 |
| Mar 24 | 243 ± 45 | 114 ± 43 |
| Apr 18 | 216 ± 50 | 182 ± 82 |
| May 17 | 124 ± 52 | |

as important as cheatgrass on the south-facing slope.

More taxa were present on the north-facing slope than on the south-facing slope. Some of these—bluebunch wheatgrass, Sandberg bluegrass, and Cusick's bluegrass—are constituents of climax plant communities. This finding suggests that the cooler-wetter microclimate of the north-facing slope is more suited to the self-establishment and growth of these species. Similar findings have been reported from the steep slopes of earth fills elsewhere in Washington (Dillon, 1967).

Cheatgrass swards are able to exclude other plant species to a high degree (Daubenmire, 1975). One of the few plants that appears to be at all competitive with cheatgrass is tumble mustard. It is especially competitive on the south-facing slope.

Artificial earth mounds provide a way to change experimentally the microclimate experienced by plants while keeping the physical-chemical features of the rooting substrate closely similar. The slopes are large enough to allow the investigation of species interrelationships, a feature not available in greenhouse or controlled growth chamber experiments.

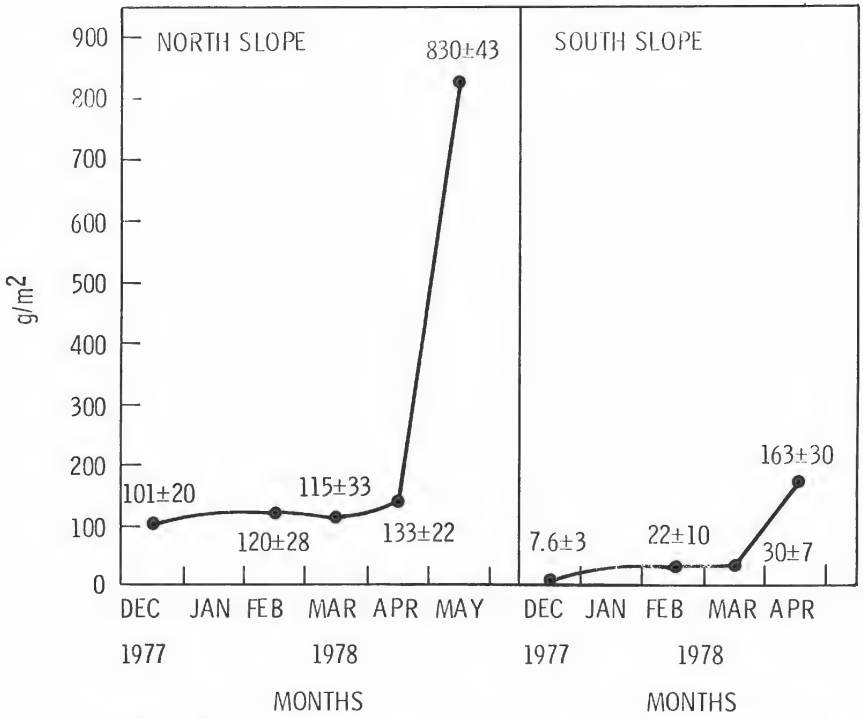


Figure 1. Seasonal changes in live phytomass on north- and south-facing slopes during the 1977-1978 growing season. Average values ± standard error.

Since its introduction to North America from Europe, cheatgrass has invaded and persisted on thousands of acres of dry rangelands. It apparently has little competition from the native plants on disturbed ground. Although cheatgrass is held in low esteem by livestock raisers, it can provide a self-sustaining ground cover that inhibits soil erosion. In arid lands where land is not intended for livestock grazing, such as shallow land burial sites for chemical wastes, cheatgrass would seem to offer a quick and effective way to establish a self-sustaining plant cover capable of resisting soil erosion.

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# Repopulation and Food Habits of Peromyscus maniculatus on a Burned Sagebrush Desert in Southeastern Idaho

## Abstract

During October 1975 and May 1976, small mammals were trapped on burned, control, and burned-soil accumulation areas of sagebrush desert following a fire in September 1974. Although six species of rodents were trapped on the study areas, deer mice (*Peromyscus maniculatus*) constituted 87 percent of the total sample. The kangaroo rat (*Dipodomys ordii*) was the only species which was more abundant in the burned areas than in the control areas. Number of deer mice per trap night, an index of relative density, increased from 0.00 and 0.005 in 1975 to 0.01 and 0.03 in 1976 in the burned and burned-soil accumulation areas, respectively. The control areas had trap-night indices for deer mice of 0.05 in 1975 and 0.08 in 1976. The diets of deer mice in May 1976 from burned and control areas indicated an intense and similar reliance on a few food items but were statistically different ($P < 0.05$). Insects provided over 90 percent of the diet. Vegetation differences between the burned and control areas were not reflected in the spring diet. Studies on seasonal food habits are needed to explain the effects of fire on small mammal repopulation of a desert ecosystem.

## Introduction

During September 1974, a fire destroyed all the above-ground vegetation on 300 ha at the Idaho National Engineering Laboratory (INEL) Site, Butte County, in southeastern Idaho (Fraley *et al.*, 1976). The area contained big sagebrush-bluebunch wheatgrass (*Artemisia tridentata-Agropyron spicatum*) and big sagebrush-squirreltail grass (*A. tridentata- Sitanion hystrix*) vegetation types prior to the burn. The species composition and densities of the rodent populations prior to the burn were not known.

Much literature is available on the effects of forest and grass fires on rodent populations (Krefting and Ahlgren, 1974; Cook, 1959; Tester, 1965). However, information is limited on the effects of fire on rodent populations in a desert shrub community (Chew *et al.*, 1958). There is also a paucity of information on the effects of fire on rodent food sources and, subsequently, on rodent repopulation of a burned area. Therefore, a study was conducted to judge the effects of fire in a desert sagebrush community on rodent food habits.

## Study Area

The study was conducted on the INEL Site which covers an area of 2315 $km^2$ and is located on the cool desert shrub biome along the western edge of the upper Snake River Plain. The topography is flat to rolling, with an average elevation of 1470 m. Annual precipitation averages 18-20 cm and temperatures range from –42 to 39°C, with an annual average of 6°C. Vegetation is dominated by desert shrubs, primarily big sagebrush (Harness and West, 1973).

One study site was located on the burned area, and another was established on an adjacent unburned area which served as a control. Vegetation on the control area con-

sisted of *Artemisia tridentata-Agropyron spicatum* and *A. tridentata-S. hystrix* vegetation types. Other important species on the control area were thickspike wheatgrass (*Agropyron dasystachyum*), textile onion (*Allium textile*), goosefoot (*Chenopodium* sp.), few-flowered eriastrum (*Eriastrum sparsiflorum*), and Hood's phlox (*Phlox hoodii*) (Fraley *et al.*, 1976). Vegetation in the burned area during 1975 consisted primarily of bluebunch wheatgrass, few-flowered eriastrum, Hood's phlox, perennial mustard (*Schoenocrambe linifolia*), and western stickseed (*Lapulla redowskii*) (Fraley *et al.*, 1976). During 1976, tumbleweed (*Salsola kali*) and halogeton (*Halogeton glomeratus*) increased in importance. During 1975, the biomass estimates for both areas were similar. In 1976, the non-sage biomass was significantly greater ($P < 0.05$) in the burned area than in the control area and was attributable to an increase in annuals, particularly tumbleweed and halogeton (Fraley, 1978). Big sagebrush did not occur on the burned site in 1975 and 1976. There appeared to be no difference in vegetation diversity between the burned and control areas in 1976. More bare ground was present in the burned area (84 vs. 75 percent) than in the control area (51 vs. 59 percent) in 1975 and 1976, respectively (Fraley, 1978).

#### Methods

Two 400 m transects were located in the burned area and two in the control area (Fraley *et al.*, 1976). One transect was also established in an area of soil accumulation adjacent to the burned area. The soil accumulation area was also burned, but woody parts of vegetation remained. This site acted as a wind break where wind-blown soil from the burn area accumulated. Twenty permanent stations were located on each burn and control transect at 20 m intervals. Thirty temporary stations were placed on the soil accumulation area at 20 m intervals.

Traps were set during October 1975 and May 1976 on the burn area, control area, and soil accumulation area. Two Museum Special snap traps and one McGill rat trap were placed at each station and baited with a peanut butter-oatmeal mixture. One trap was placed on the center of the transect and the other traps were placed 1.5 m each side of the center line. Traps were set for three consecutive nights in 1975 and five consecutive nights in 1976 for a total of 990 and 1650 trap nights, respectively. Traps were prebaited for three consecutive nights before trapping.

Deer mice (*Peromyscus maniculatus*) gastrointestinal (GI) tracts were sent to Colorado State University Composition Analysis Laboratory for analysis of food content. Data were recorded on sex, age (adult or subadult), and weight, and were categorized by capture location (burned or control). Sex was determined during dissection and age was determined by body weight (mice less than 15 g were assumed to be subadult). One hundred twenty-nine deer mice GI tracts from the control area and 65 deer mice GI tracts from the burned and soil accumulation areas were analyzed. All samples were from the 1976 trapping period. Mice from the soil accumulation areas were categorized as burned area samples because vegetation patterns in both areas were similar and increased the sample of burned area rodents for food habits analyses. Stomach samples from each of six categories (control area male, control area female, and control area subadult, and burned area male, burned area female, and burned area subadult) were combined, and five slides were made for each category. Fields on microscope slides were viewed under a binocular microscope at 100x for

identifiable food fragments. Forty fields were examined per slide, and the percent relative density of food fragments was recorded. Plant fragments were quantified as described by Sparks and Malecheck (1968). The percentage of classified food fragments approximated the percentage relative dry weights of food categories in the diet (Dearden *et al.*, 1975).

Percent similarity between diets was calculated using Kulcyznski's coefficient of community (Oosting, 1956) for food items comprising $\geq$ 2 percent of the diet. A Chi-square contingency table was used to determine differences in diets between burn area and control area deer mice (Snedecor and Cochran, 1972). A diversity index was also calculated for diets of burned and control area rodents using the Shannon-Weiner formula (Collier *et al.*, 1973). Level of significance was established as $P < 0.05$ for all analyses.

### Results and Discussion

A total of 288 rodents representing six species (deer mouse, least chipmunk [*Eutamias minimus*], kangaroo rat [*Dipodomys ordii*], western harvest mouse [ *Reithrodontomys megalotis*], northern grasshopper mouse [*Onychomys leucogastor*], and Townsend's ground-squirrel [*Spermophilus townsendi*]) was captured during the two trapping periods (Table 1). The only rodents trapped in 1975 from the burned area were two kangaroo rats. During 1976, 26 rodents were trapped on the burned area. Eleven rodents were trapped in 1975 in the burned-soil accumulation area compared to 82 in 1976 (Table 1). Although only 13 kangaroo rats were captured both years, all were trapped on the burned sites. Apparently, removal of the brush species by fire and the accumulation of soil on some burned sites provided favorable habitat for kangaroo rats. Least chipmunks, western harvest mice, northern grasshopper mice and Townsend's ground-squirrels were captured too infrequently (Table 1) to enable comparisons between study areas. Generally, the numbers of each species trapped in all study areas increased in 1976 compared to 1975. This increase reflected the additional trap nights in 1976.

TABLE 1. Number of all rodents trapped from burn, control, and soil accumulation areas on the Idaho National Enginering Laboratory Site during October 1975 and May 1976 and the number of **Peromyscus maniculatus** captured per trap night.

| | Number captured | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Peromyscus maniculatus* | | *Eutamias minimus* | | *Dipodomys ordii* | | *Reithrodontomys megalotis* | | *Onychomys leucogaster* | | *Spermophilus townsendi* | |
| Location | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 |
| Burn | 0 (0.00) [a] | 22 (0.01) | 0 | 0 | 2 | 3 | 0 | 1 | 0 | 0 | 0 | 0 |
| Control | 47 (0.05) | 134 (0.08) | 5 | 5 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 |
| Soil Accumulation | 5 (0.005) | 43 (0.03) | 3 | 1 | 1 | 7 | 0 | 5 | 0 | 0 | 0 | 0 |
| Totals | 52 | 199 | 8 | 6 | 3 | 10 | 0 | 7 | 0 | 2 | 0 | 1 |

[a] ( ) = number per trap night.

The majority (87 percent) of rodents captured during both years were deer mice. Deer mice were most abundant in the control area followed by the soil accumulation and burned areas (Table 1). Indices of deer mice densities (number per trap night) increased in all study areas in 1976 over 1975. The greatest increase in deer mice density occurred in the soil accumulation areas (Table 1).

No deer mice were trapped on the burned area during October 1975, but in May 1976, 22 were captured. During the respective years 1975 and 1976, 47 and 134 deer mice were captured on the control areas. Cook (1959) found that *P. maniculatus* populations attained higher densities in brush areas than in open grasslands, areas which may correspond to the control and burned areas in this study. Five deer mice were captured in 1975 and 43 in 1976 on the soil accumulation area.

Food habits data for deer mice indicated a heavy reliance on insects (Table 2). Deer mice are omnivorous and consume a variety of plant and animal foods, with their diet reflecting local availability of foods at various seasons (Martin *et al.*, 1961). All food habit determinations were made on deer mice captured in late May, a period when insects were probably most abundant. Insects probably were the most available food source during the entire study period.

TABLE 2. Percent relative density ($\bar{X}\pm SD$) of the food categories found in the gastrointestinal tracts of **Peromyscus maniculatus** from control and burned areas on the Idaho National Engineering Laboratory Site, May 1976.

| | Control ($\bar{X}$+SD) | | | | Burn ($\bar{X}$+SD) | | | |
|---|---|---|---|---|---|---|---|---|
| | Male (50)[a] | Female (44) | Juvenile (35) | Total Population (129) | Male (29) | Female (29) | Juvenile (7) | Total Population (65) |
| Lepidoptera Larvae | $71 \pm 6$ | $49 \pm 3$ | $73 \pm 9$ | $64 \pm 13$ | $31 \pm 7$ | $23 \pm 9$ | $57 \pm 5$ | $37 \pm 16$ |
| Coleoptera adult | $20 \pm 3$ | $45 \pm 3$ | $10 \pm 2$ | $25 \pm 15$ | $60 \pm 8$ | $65 \pm 6$ | $36 \pm 8$ | $54 \pm 15$ |
| Araneida | $2 \pm 1$ | $3 \pm 2$ | $3 \pm 2$ | $3 \pm 2$ | $1 \pm 1$ | $0.5 \pm 0.7$ | $0.3 \pm 0.7$ | $1 \pm 1$ |
| Formicidae | $2 \pm 2$ | 0 | $9 \pm 3$ | $4 \pm 4$ | 0 | 0 | 0 | 0 |
| Feather | $2 \pm 2$ | $2 \pm 2$ | 0 | $1 \pm 2$ | 0 | 0 | 0 | 0 |
| Orthoptera | $0.4 \pm 0.5$ | $0.2 \pm 0.5$ | $0.8 \pm 0.7$ | $0.5 \pm 0.6$ | 0 | 0 | 0 | 0 |
| Plants | 0 | $1 \pm 1$ | $4 \pm 3$ | $1 \pm 2$ | $8 \pm 3$ | $11 \pm 4$ | $6 \pm 5$ | $8 \pm 4$ |
| Seeds | 0 | 0 | $0.7 \pm 0.6$ | $0.2 \pm 0.5$ | 0 | 0 | 0 | 0 |

[a] ( ) = number of deer mouse stomachs combined for microscopic analysis.

Coleoptera adults and Lepidoptera larvae accounted for over 90 percent of the diet of deer mice from both the burned and control areas (Table 2). The Shannon-Weiner diversity indices were 1.38 and 1.32 for diets of deer mice captured in control and burned areas, respectively. These low diversity indices indicate that deer mice from both the burned and control areas depended upon a small number of food items. No significant difference (paired t-test) was found in the diversity indices of burned versus control area rodents. Kulcyznski's coefficient of community indicated a 66 percent similarity in the diets of burn and control rodents. Although this figure represents a high percentage overlap, the diets of deer mice from the burned and control areas were statistically different ($P < 0.05$). The diet of control area deer

mice contained about half the amount of Coleoptera adults and nearly twice the amount of Lepidoptera larvae as the burned area rodents (Table 2). Comparisons of the two major food items in the diet indicated significant differences ($P < 0.05$) between burn and control deer mice. The abundance of Coleoptera adult and Lepidoptera larvae on the study areas was not measured. Thus, the reason for the differences in occurrence of the two items in the gastrointestinal tract is unclear. Perhaps the vegetation cover and species differences between the two areas (Fraley, 1978) was a factor affecting the density of the two groups of insects and consequently the diets of the deer mice. *Formicidae* and *Orthoptera* availability was also likely a function of the vegetation composition of burned and control areas. Ants (*Formicidae*) and crickets or grasshopers (*Orthoptera*) did not occur in the diets of burned area deer mice, but comprised respectively 4 and 5 percent of the relative density of control deer mice diets (Table 2).

The occurrence of plants in the diet of both control and burned area deer mice was less than 10 percent, although deer mice collected from the burned site consumed significantly ($P < 0.05$) more plant material than control deer mice (Table 2). This finding may reflect a lack of new growth during 1976 of sagebrush and grasses on the study areas (Fraley, 1978): *Artemisia spp.* represented over 90 percent of the plants consumed by deer mice from both areas. These results, then, are contrary to vegetation data collected in 1976, which indicated *Artemisia spp.* occurred only on the control grids (Fraley, 1978). Since deer mice have home ranges from 0.1 to over 1.2 ha (Lechleitner, 1969), perhaps mice inhabiting the burned area fed in adjacent areas containing sagebrush.

Since the degree of movement by deer mice between control and burned areas was not studied, one cannot conclude that deer mice from the burned area did not forage in the adjacent control areas. Statistical analyses of food habits, however, indicate that deer mice from the burned and control areas are different populations with respect to diet. The differences in vegetative composition in the burned and control areas were not reflected in deer mice diets. Still, vegetative composition could account for the availability of insects and as a consequence have an indirect effect on the food habits of deer mice from the burned and control areas. Further food habits data on a seasonal basis would enable better evaluation of the use of food habits to help explain the effects of fire on small mammal densities. Combining seasonal, long-term food habits data with vegetation analysis and rodent trapping should enable investigators to estimate the relationships of plant succession and rodent repopulation in desert ecosystems following fires. In a slow recovery area, information of this type is useful to allow man to predict the adverse impacts of a disturbance such as fire.

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# Effects of Supersaturated Dissolved Atmospheric Gases on Northern Squawfish, Ptychocheilus oregonensis

## Abstract

Northern squawfish, *Ptychocheilus oregonensis*, were confined in shallow tanks for 12 days to study their tolerance to various concentrations of total dissolved atmospheric gases (TDG). The TDG concentrations ranged from 100 to 126 percent of saturation—levels that occur in the Columbia and Snake Rivers downstream from dams during periods of high flow. Mortality did not occur in tests at or below 110 percent of saturation, but 32 percent of the fish succumbed in 12 days at 117 percent of saturation and 100 percent died in 20 hours at 126 percent of saturation. Average daily food consumption of squawfish decreased in proportion to increased saturation levels. At 100 percent of saturation (normal gas content), 14.2 g of food per fish per day were consumed; at 117 percent, 6.2 g; and at 120 percent, only 2.3 g per fish per day were consumed.

Field studies (1974 to 1976) indicated squawfish in the Snake River may not be seriously affected by supersaturation (from 117 to 141.5 percent of saturation). Gill-net drifts in the tailrace of dams showed that most squawfish were below the 3-m depth; therefore, they were at equilibrium and were unaffected by nitrogen supersaturation in the river. High TDG levels did not appear to hinder movement within 92 km of the study area. Purse seining adjacent to dams during spill closures indicated squawfish were actively feeding on fingerling salmon but probably did so from an equilibrated depth.

## Introduction

Northern squawfish, *Ptychocheilus oregonensis*, have attracted the interest of many investigators because they are a major predator on valuable species of Pacific salmon, *Oncorhynchus* sp., and trout, *Salmo* sp. Hamilton *et al.* (1970), for example, reported that predation by squawfish was severe enough to preclude the use of Lake Merwin Reservoir, Washington, as a rearing area for coho salmon, *O. kisutch*. Brett and McConnell (1950), calculating losses of sockeye salmon, *O. nerka*, juveniles from Lakelse Lake, British Columbia, estimated that the consumption rate per squawfish was 140 salmon fingerlings per year. Thompson (1959) found that squawfish in the Columbia River were largely opportunistic in their feeding habits—7.5 percent of the squawfish stomachs examined for one year contained juvenile salmon, but in areas where migrating juvenile salmonids were prevalent, 51 percent of the adult squawfish fed on them.

Squawfish are present in large numbers in the lower Snake River, a principal

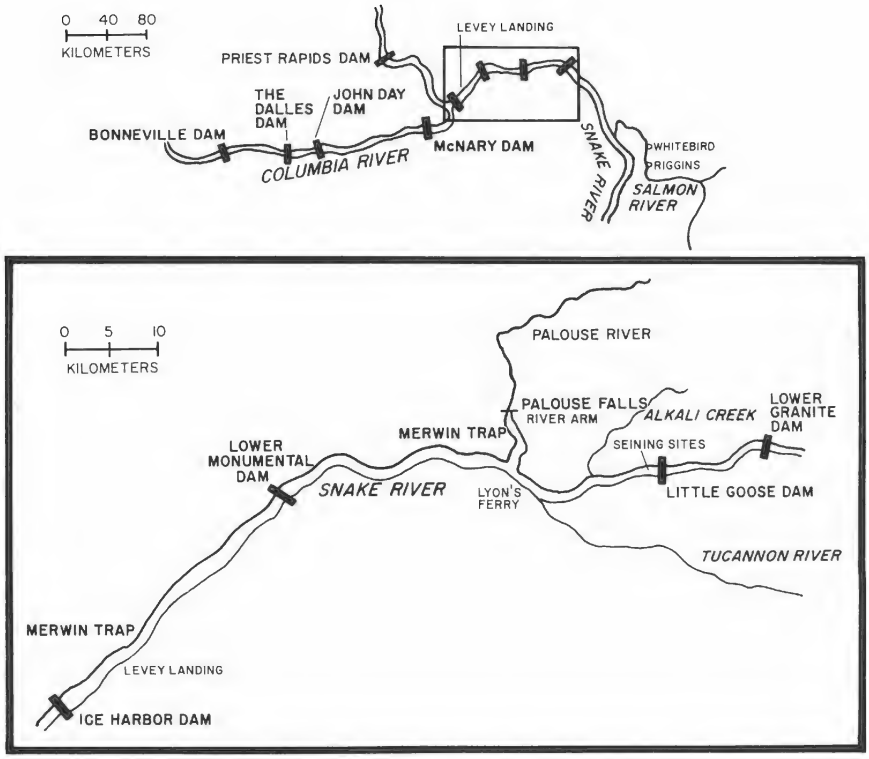


Figure 1. Dams on the Snake and Columbia Rivers from Little Goose to Bonneville. Detail shows squawfish catch areas.

tributary of the Columbia River (Fig. 1). Each spring millions of seaward migrating juvenile chinook salmon, *O. tshawytscha*, and steelhead trout, *S. gairdneri*, pass through the lower Snake River and could conceivably suffer substantial losses by squawfish predation. Long and Krcma (1969) measured a 33 percent loss of fingerlings related to predation by squawfish in the backroll and slackwater areas of the tailrace at Ice Harbor Dam.

In addition to losses caused by predation, supersaturation of dissolved gases in the water resulting from spilling at hydroelectric dams has caused significant losses in the past ten years of stocks of anadromous fish in the Columbia and Snake Rivers (Ebel, 1969, 1971). The relationship between squawfish predation and supersaturation of total dissolved atmospheric gases (TDG) was unknown at the time of Ebel's studies. Knowledge of the relationship between supersaturated water and squawfish predation could be important in making management decisions on dissolved gas control measures that are recommended by the fishery agencies. Meekin and Turner (1974) found that predation capabilities were substantially reduced at dissolved nitrogen concentrations of 120 percent of saturation and that mortalities occurred at 135 percent.

In our tests, we studied mortality rates for squawfish at various concentrations of supersaturation along with food consumption differences among the groups. A preliminary report on the first phase of this research was published by Bentley *et al.* (1976). Complete results of these tests and field observations of migration and feeding habits of squawfish in the Snake River are reported in the present paper.

## Methods

### Laboratory Tests

Adult squawfish (100) for the laboratory study were captured in the Snake River and transported by tank truck to the Northwest and Alaska Fisheries Center, National Marine Fisheries Service (NMFS), in Seattle, Washington. These fish were acclimated to the laboratory water at 10°C and normal TDG saturation (100 percent) and starved for 16 days before being introduced directly into the test tanks containing supersaturated water.

Six tests were conducted at average TDG concentrations of 126.1, 120.4, 117.2, 110.3, 107.2, and 99.8 percent of saturation. Simultaneous replicates were made of tests at 117.2, 110.3, and 99.8 percent of saturation. Nitrogen and oxygen concentrations were held to $\pm$ 4 percent of the TDG saturation value; standard deviations for daily dissolved gas data ranged from 0.5 to 3.1 percent TDG for the test duration of 12 days. All test tanks were 1.2 m in diameter with water depths of 25 cm (potential hydrostatic compensation 0.025 atmosphere of pressure, or about 2.5 percent of saturation). Water flow was maintained at 7.5 liter/min at 10°C $\pm$ 1° C. Lighting was controlled to simulate natural sunrise and sunset.

Tests began on 17 April 1974, and were conducted with about 10 fish per tank. The mean length and weight of the test fish at introduction was 364 mm and 534 g, respectively. Prior to the actual tests, a sample population was fed to determine the maximum weight of food an unstressed fish might consume in a 2-wk period. On the basis of food intake of the sample population, we established a daily ration for test groups of four dead eulachon, *Thaleichthys pacificus* (average size: 170 mm, 30 g), and one live steelhead trout (average size: 80 mm, 21 g) for each test tank. One-half of the eulachon introduced as food were cut in half to accommodate the smaller squawfish.

During the tests, fish groups were observed for behavioral changes, with particular regard to their food intake. Daily measurements of dissolved gas concentrations were performed, using gas chromatography calibrated for nitrogen plus argon with a manometric blood gas analyzer (Van Slyke and Neil, 1924) and for oxygen with the Winkler titration (American Public Health Association *et al.*, 1971). Dead fish were taken from test tanks twice daily, weighed, measured, and examined for signs of gas bubble disease. All fish were examined at the end of the test period for internal and external signs of gas bubble disease.

### Field Observations

During 1974, 1975, and 1976, adult squawfish were collected from the Snake River to examine their food intake, movement, and vertical distribution in relation to varying levels of dissolved gas supersaturation in the river. Captured fish were anesthetized, measured, and checked for food intake and signs of gas bubble disease symptoms.

They were then marked and returned to the river. Marking was accomplished with either a Floy anchor tag, FD67,[1] or branding (Mighell, 1969).

Squawfish were collected from the Snake River by purse seines and gill nets in the tailrace of Little Goose Dam. They were also collected from Lake Merwin traps (Hamilton *et al.*, 1970) in the Palouse River Arm, 20 km downstream from the dam, and at Levey Landing, 92 km downstream from Little Goose Dam (Fig. 1). The Merwin trap in the Palouse River Arm was operated seasonally from November 1973 to 1 July 1976 and the trap at Levey Landing, from October 1974 to 1 July 1976. Purse seining was done at Little Goose Dam from 24 April to 8 August 1974, and at Lower Granite Dam from 6 May to 23 June 1976. Gill-net drifts in the tailrace area of Little Goose Dam were made from 25 April to 22 May 1975.

Purse seining was done with a net 4.6 m deep and 160 m long; it was operated from a power-driven barge using a technique similar to that described by Durkin and Park (1967). The drifted gill net was 91.4 m long by 6.7 m in depth with a stretched mesh of 6.35 cm. The technique was to get as close to the spill as possible. When the boat was in position, the engine was put in reverse. While the boat was backing across the wake of the spill, the gill net was fed into the water through rollers in the bow. After the net was all out, the boat drifted with the net for about 1200 m downstream. The net was usually set perpendicular to the spill current.

Food intake was measured from fish taken in 1976 by purse seines in the tailrace of Lower Granite Dam. Accurate measures were not possible at Little Goose Dam during the first two years of the study because high spill and turbulence during the fingerling seaward migration prevented adequate sampling in the tailrace. By 1976, a method of controlling spill at Lower Granite Dam was developed wherein the spill was shut off for short periods to permit adequate sampling in the tailrace.

Depth distribution of squawfish was determined from samples taken by gill nets in 1975. A black marker line was sewed at the 3-m depth to ascertain with accuracy whether a captured squawfish was above or below the depth which generally insured safety from the effects of supersaturation in the Snake River (Ebel, 1969, 1971). We assumed depth distribution was similar in 1976 to that measured in 1975.

Water samples were taken biweekly between April and August from 1974 to 1976 to study the concentration of dissolved gases in the Snake River. Analyses were made at the NMFS Northwest and Alaska Fisheries Center.

## Results

### Laboratory Tests

*Mortality and Signs of Gas Bubble Disease.* Substantial mortality of squawfish occurred in tests at high supersaturation concentrations but did not occur in tests at or below 110 percent of saturation. One hundred percent mortality occurred in 20 h at 126 percent of saturation; 60 percent loss occurred within the 12-d test period at a concentration of 120 percent; and 32 percent loss occurred within the 12-d test period at 117 percent of saturation. Lethal exposure times to 10 and 50 percent mortality ($LE_{10}$ and $LE_{50}$) for squawfish are compared in Table 1 with $LE_{10}$ and $LE_{50}$ values

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

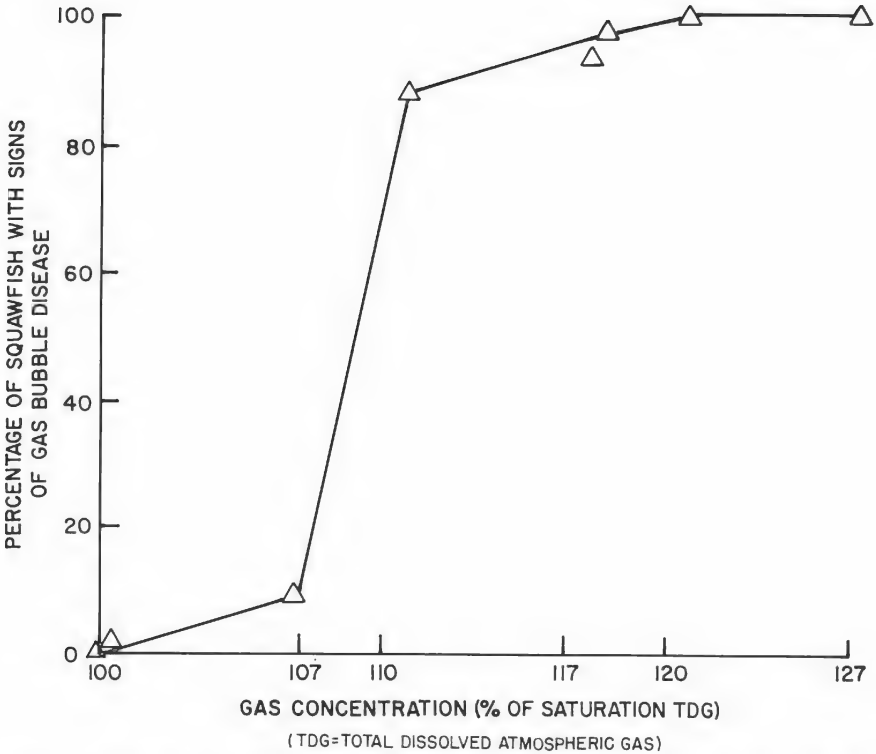


Figure 2. Percentage of squawfish with signs of gas bubble disease after death or after surviving 12 days of exposure to various concentrations of dissolved gas in laboratory tests.

established for their potential salmonid prey (Dawley and Ebel, 1975; Dawley *et al.*, 1976). Evidently squawfish are more tolerant to supersaturation of dissolved gas than juvenile steelhead trout and spring chinook salmon, but they are much less resistant than fall chinook salmon fry.

Signs of gas bubble disease were found in all fish exposed to 126, 120, and 117 percent of saturation (Fig. 2). Of the squawfish exposed to 110 percent of saturation,

TABLE 1. Comparison of lethal exposure times to 10 and 50 percent mortality ($LE_{10}$ and $LE_{50}$) for squawfish and potential salmonid prey at different concentrations of dissolved gas in shallow tanks.

| Total dissolved gas concentration (% saturation) | Adult squawfish (364 mm, 534 g) 10°C | | Juvenile steelhead trout (135 mm, 20 g) 15°C | | Juvenile spring chinook salmon (120 mm, 15 g) 15°C | | Juvenile fall chinook salmon (42 mm, 0.4 g) 10°C | |
|---|---|---|---|---|---|---|---|---|
| | $LE_{10}$ (h) | $LE_{50}$ (h) | $LE_{10}$ (h) | $LE_{50}$ (h) | $LE_{10}$ (h) | $LE_{50}$ (h) | $LE_{10}$ (h) | $LE_{50}$ (h) |
| 115 | — | — | — | — | — | — | 480 | 1128 |
| 117 | 115 | >228* | 26 | 33 | 19 | 27 | — | — |
| 120 | 41 | 233 | 10 | 14 | 11 | 14 | 168 | 528 |
| 126 | 19 | 20 | — | — | — | — | — | — |

*Test groups sustained a mean of 29% mortality in 228 h.

89 percent had gross signs of gas bubble disease; 1 of 10 fish exposed to 107 percent of saturation exhibited signs. No signs were noted among the fish exposed to 100 percent saturation. Gross gas bubble disease signs included hemorrhage and subcutaneous gas blisters over large areas of the body. All fish showing signs of gas bubble disease exhibited greatly distended gas blisters between the fin rays. Exophthalmia ("popeye") occurred in only two fish. Gaseous emboli were noted in the blood vessels of at least one gill arch in all dead fish. Emboli were also observed in the gill filaments of all squawfish surviving the test at 120 percent of saturation and many surviving the tests at 117 percent. Emboli within the gill filaments were not detected in squawfish exposed to lower supersaturation concentrations.

*Feeding Activity.* Active feeding decreased by about 84 percent, from an average of 14.3 g of food per fish per day for squawfish exposed to 100 percent (normal) saturation to an average 2.3 g of food per fish per day when squawfish were exposed to 120 percent of saturation (Fig. 3). These data also indicated that food uptake by

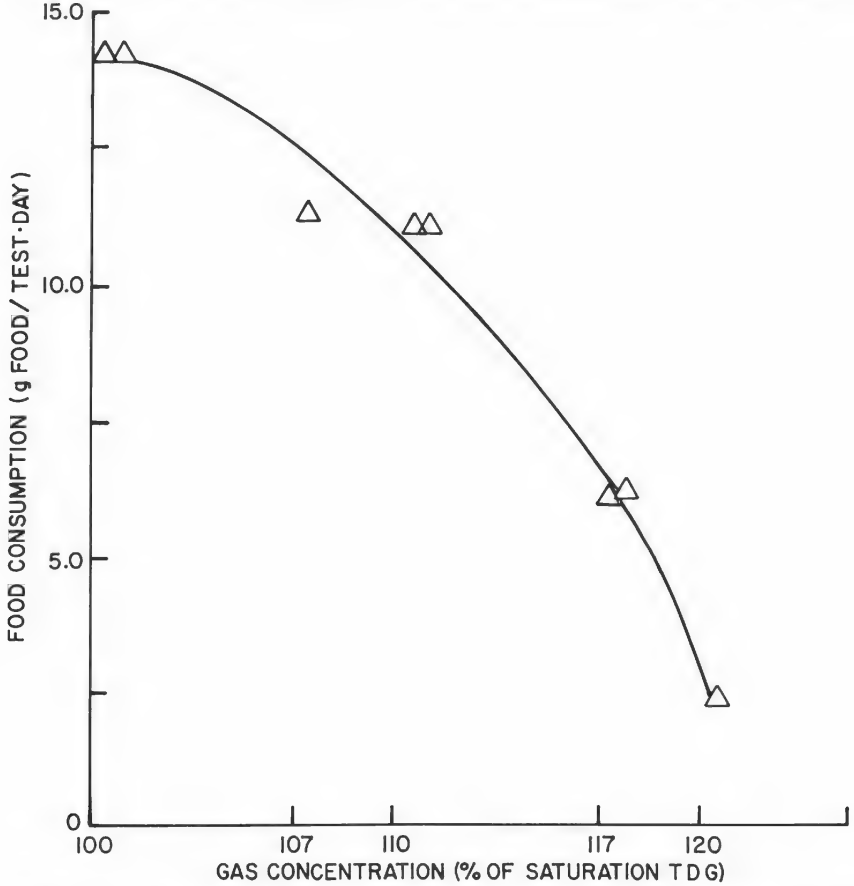


Figure 3. Average daily food consumption of squawfish exposed to different dissolved gas concentrations for 12 days in laboratory tests (TDG = total dissolved atmospheric gas).

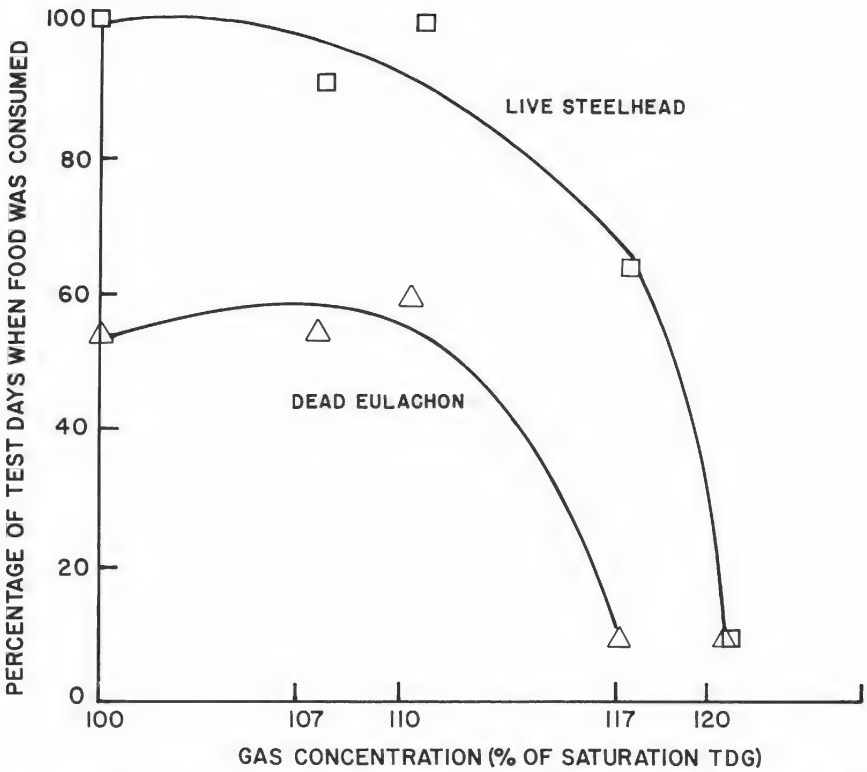


Figure 4. Percentage of days during laboratory test when food ration was completely consumed by squawfish in relation to different dissolved gas concentrations (TDG = total dissolved atmospheric gas).

squawfish would be reduced from normal by about 50 percent when the concentration of TDG reached 115 percent of saturation. At concentrations below 117 percent, squawfish showed a preference for consuming live steelhead trout rather than dead eulachon (Fig. 4). Squawfish held at 120 percent of saturation consumed no live steelhead trout after the first day of testing. At 117 percent of saturation, the consumption of live steelhead trout was reduced 40 percent compared to the control.

The inability or unwillingness of squawfish stressed by supersaturation to catch and consume live steelhead trout may be affecting predation on juvenile salmonids migrating downstream in the Columbia and Snake Rivers. Our laboratory tests, however, were accomplished in shallow tanks allowing no potential hydrostatic compensation from the effects of supersaturation. Measurements made on the river in 1976, where there was sufficient depth to equilibrate, provided additional data on predation rate in supersaturated water. These data will be discussed later.

### Field Observations

*Movements of Squawfish Relative to Dissolved Gases.* A total of 23,046 squawfish were captured, tagged, and released from the trap in the Palouse River Arm from

November 1973 to 1 July 1975. A total of 2729 squawfish were captured, tagged, and released from the trap at Levey Landing from October 1974 to 1 July 1975. Between April 1974 and 1 July 1975, 2859 squawfish were collected, tagged, and released from purse-seine and gill-net sampling below Little Goose Dam. Subsequent recaptures of tagged fish provided data on their migration behavior during varying concentrations of supersaturation (up to 141.5 percent of saturation) in the Snake River in 1974 and 1975 (Table 2).

TABLE 2. Temperature, dissolved gas concentrations, spill volume, and total water flow at Lower Monumental and Little Goose Dams from April to August 1974 and from April to July 1975.

| | Little Goose Dam forebay Saturation (%) | | | | | | Lower Monumental Dam forebay Saturation (%) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Temp (°C) | $O_2$ | $N_2$ + Ar | TDG* | Spill** | Total river flow (km³/s) | (°C) Temp | $O_2$ | $N_2$ + Ar | TDG* | (km³/s) Spill** | Total river flow (km³/s) |
| 1974 | | | | | | | | | | | | |
| 4/19 | 8.3 | 99.6 | 101.4 | 101.0 | 2.43 | 3.71 | 8.5 | 117.8 | 122.1 | 120.9 | 2.35 | 4.25 |
| 4/23 | 9.6 | 102.5 | 106.8 | 105.8 | 1.73 | 3.68 | 9.9 | 130.8 | 134.6 | 133.3 | 1.67 | 3.57 |
| 5/7 | 11.6 | 105.9 | 110.3 | 109.2 | 2.72 | 4.59 | 12.1 | 130.8 | 135.8 | 134.2 | 2.69 | 4.64 |
| 5/21 | 11.4 | 98.5 | 104.1 | 102.8 | 0.48 | 2.35 | 11.3 | 114.2 | 121.5 | 119.7 | 0.42 | 2.26 |
| 6/4 | 12.2 | 99.2 | 102.9 | 102.0 | 2.60 | 4.55 | 11.9 | 127.9 | 141.1 | 137.7 | 2.55 | 4.50 |
| 6/19 | 12.8 | 102.4 | 111.5 | 109.4 | 6.45 | 8.49 | 12.5 | 128.7 | 143.8 | 140.0 | 6.22 | 8.32 |
| 7/2 | 16.9 | 99.5 | 106.8 | 105.1 | 0.0 | 3.57 | 16.7 | 124.6 | 131.8 | 129.8 | 1.87 | 3.77 |
| 7/16 | 17.4 | 103.4 | 106.7 | 105.9 | 0.54 | 1.78 | 19.0 | 102.4 | 106.4 | 105.5 | 0.08 | 1.93 |
| 7/30 | 24.5 | 117.7 | 110.3 | 111.5 | 0.0 | 1.33 | 23.2 | 110.3 | 106.7 | 107.2 | 0.0 | 1.24 |
| 8/13 | 21.7 | 99.4 | 104.9 | 103.7 | 0.0 | 1.25 | 21.7 | 101.8 | 105.8 | 104.9 | 0.0 | 1.22 |
| 1975 | | | | | | | | | | | | |
| 4/8 | 7.6 | 121.6 | 113.8 | 115.2 | 0.42 | 1.64 | 7.6 | 122.2 | 110.6 | 112.9 | 0.0 | 1.81 |
| 4/22 | 9.9 | 128.4 | 118.0 | 119.9 | 0.70 | 2.54 | 9.6 | 120.1 | 114.5 | 115.5 | 0.76 | 2.56 |
| 5/6 | 10.0 | 112.2 | 111.4 | 111.4 | 0.53 | 2.40 | 10.5 | 124.2 | 125.0 | 124.5 | 1.10 | 2.40 |
| 5/20 | 13.4 | 124.7 | 128.1 | 125.4 | 3.85 | 5.12 | 12.7 | 138.2 | 139.6 | 138.3 | 3.37 | 4.64 |
| 6/3 | 13.2 | 112.9 | 118.5 | 117.0 | 3.37 | 5.26 | 14.0 | 128.3 | 134.5 | 132.7 | 3.05 | 4.92 |
| 6/17 | 12.8 | 114.0 | 121.1 | 119.3 | 2.86 | 5.23 | 13.9 | 130.4 | 140.9 | 138.0 | 1.78 | 3.68 |
| 7/1 | 13.5 | 116.8 | 121.9 | 120.5 | 1.58 | 3.42 | 14.1 | 137.6 | 143.4 | 141.5 | 1.30 | 3.17 |

*TDG = Total dissolved atmospheric gases.

**Water flow data entered in thousands of cubic meters per second (km3/s).

Most upstream movement of squawfish occurred after spilling had ceased and gas concentrations had returned to normal. Of approximately 17,000 fish tagged in the Palouse River Arm between April and June 1974, only four were recovered in the tailrace of Little Goose Dam during supersaturation conditions, compared to recovery of 101 after gas concentrations had returned to normal (Table 3). However, substantial numbers of squawfish did move downstream during periods of high dissolved gas concentrations. Seventeen of the fish tagged at Little Goose Dam were recovered downstream in the trap at the Palouse River Arm and three further downstream in the trap at Levey Landing; i.e., 20 km and 92 km downstream, respectively, from the tagging site. Twenty-six of the fish tagged in the Palouse River Arm were subsequently recovered downstream in the trap at Levey Landing.

All downstream recoveries were made when concentrations of TDG were high. Obviously these fish must have traveled at a depth which compensated for high

TABLE 3. Movements of squawfish between areas in 1974 and 1975 during periods of high dissolved gases (>120% of saturation) and low dissolved gases (<120% of saturation).

| Area | No. squawfish moving in high TDG* concentrations (>120% of saturation) April through June | Distance between sites (km) | Average no. days since tagged | No. squawfish moving in lower or normal TDG concentrations (<120% of saturation) July through March | Average no. days since tagged |
|---|---|---|---|---|---|
| Little Goose Dam to Palouse Trap | 17 | 20 | 215 | 31 | 111 |
| Little Goose Dam to Levey Trap | 3 | 92.5 | 24 | 0 | — |
| Palouse Trap to Little Goose Dam | 4 | 20 | 207 | 101 | 141 |
| Palouse Trap to Levey Trap | 26 | 72.7 | 166 | 4 | 168 |
| Levey Trap to Little Goose Dam | 2 | 92.5 | 18 | 0 | — |
| Levey Trap to Palouse Trap | 2 | 72.7 | 155 | 0 | — |
| | 54 | | | 136 | |

*TDG = total dissolved gas.

dissolved gas concentrations recorded near the surface at the time. If they had traveled in the upper 3 m of water where gas concentrations would have been greater than 110 percent of saturation, they could not have survived the journey (based on laboratory test data).

*Depth Distribution.* Gill nets drifted through the tailrace of Little Goose Dam from 25 April through 22 May 1975 captured 290 squawfish in eight drifts (Table 4). Dissolved gas levels during this period ranged between 116 and 130 percent of saturation. Only five fish were above the 3-m marker, indicating that less than 2 percent were in the lethal area of supersaturated concentrations at the time of capture.

TABLE 4. Depth at which squawfish were caught by drifting gill nets in the tailrace of Little Goose Dam from 25 April through 22 May 1975.

| Date | No. gill net drifts | No. squawfish caught | |
|---|---|---|---|
| | | Below 3-m depth | Above 3-m depth |
| April | | | |
| 25 | 3 | — | — |
| May | | | |
| 2 | 1 | 58 | 0 |
| 8 | 1 | 60 | 3 |
| 16 | 2 | 132 | 2 |
| 22 | 1 | 35 | 0 |
| Total | 8 | 285 | 5 |

However, 46 percent showed signs of gas bubble disease, suggesting that they spent part of their time during this period in surface areas.

*Feeding Activity.* We purse seined in the tailrace of Little Goose Dam in 1974 during the seaward migration of salmonids when TDG concentrations in the river were high (Table 2); 5 out of 176 squawfish taken showed evidence of feeding (Table 5). When dissolved gas content returned to near normal concentrations, 100 percent of the squawfish examined were shown to be feeding heavily on Pacific lamprey ammocetes, *Entosphenus tridentatus*, and unidentified fish (Table 5).

At Lower Granite Dam in 1976 over 2600 squawfish were captured in 32 purse seine sets during the salmonid fingerling seaward migration (Table 6). Spilling was

TABLE 5. Fishing effort, catches, and observed stomach contents of squawfish captured by purse seining in the tailrace area at Little Goose Dam during periods of high and low dissolved gas concentrations in 1974.

| Gas condition | Date | No. of sets | No. of squawfish captured | No. of squawfish containing food organisms | Type of food |
|---|---|---|---|---|---|
| High* | April 24 | 2 | 3 | 0 | — |
| | 25 | 4 | 26 | 1 | unident. fish |
| | May 3 | 1 | 22 | 0 | — |
| | 16 | 2 | 12 | 0 | — |
| | 30 | 3 | 17 | 2 | unident. fish |
| | 31 | 2 | 18 | 0 | — |
| | July 12 | 1 | 78 | 2 | unident. fish |
| | | 15 | 176 | 5 | |
| Low** | July 17 | 2 | 26 | | |
| | 18 | 3 | 398 | | |
| | 31 | 4 | 125 | | |
| | August 2 | 1 | 542 | 100 | lamprey or |
| | 6 | 1 | 699 | | examined unidentified fish |
| | 8 | 1 | 145 | | — |
| | | 12 | 1935 | 100 | |

*Concentration of dissolved gas ranged from 120 to 140% of saturation (TDG).

**Concentration of dissolved gas ranged from 105 to 107% of saturation (TDG).

TABLE 6. Fishing effort, catches, and observed stomach contents for adult squawfish (fish greater than 180 mm long) captured by purse seining in the tailrace area at Lower Granite Dam in 1976.

| Date | Purse seine sets | Total no. squawfish | | | | No. adult squawfish* | | |
|---|---|---|---|---|---|---|---|---|
| | | Eddy | Spill | Power house | Lock | Catch | With salmon | Predation index** |
| 5/6*** | 5 | 87 | 7 | 0 | 0 | 29 | 8 | 27.6 |
| 5/13 | 5 | 98 | 0 | 0 | 0 | 13 | 1 | 7.7 |
| 5/19 | 3 | 257 | 0 | 0 | 0 | 90 | 2 | 2.2 |
| 5/21 | 2 | 167 | 0 | 0 | 0 | 62 | 2 | 3.2 |
| 5/26 | 3 | 473 | 0 | 0 | 0 | 360 | 52 | 14.4 |
| 6/2 | 3 | 114 | 0 | 0 | 27 | 40 | 12 | 30.0 |
| 6/4 | 4 | 111 | 0 | 0 | 0 | 27 | 9 | 33.3 |
| 6/8 | 2 | 261 | 0 | 0 | 0 | 149 | 48 | 32.2 |
| 6/10* | 4 | 432 | 16 | 0 | 0 | 342 | 91 | 26.6 |
| 6/23 | 1 | 684 | 0 | 0 | 0 | 330 | 83 | 25.2 |
| Total | 32 | 2684 | 23 | 0 | 27 | 1442 | 308 | Avg. 21.4% |

*Longer than 180 mm.

**Index = No. of squawfish with salmon/no. of squawfish <180 mm.

***Controlled closure of spill gates.

continuous except during short periods when the spill was shut down to permit sampling. Dissolved gas concentrations ranged between 117 and 124 percent of saturation during the sampling period. Of the 1442 adult squawfish stomachs examined, 21 percent contained salmon; further examination of these stomach contents revealed that the majority of squawfish had consumed fingerling salmon before they were captured, indicating that active predation was occurring. This determination was made by examining the degree of decomposition of the prey in the digestive tract. Any decomposition would indicate predation in the wild before capture rather than feeding on fingerling salmon also captured in the seine.

*Population Estimates and Predation Rates.* During April, May, and June 1974, 17,664 squawfish were collected, tagged, and released in one small area of the Snake River (Palouse River Arm); 2583 or 15 percent were subsequently recaptured. The mean Petersen estimate (Chapman, 1952) indicated a population of about 117,600 fish. If similar numbers were present in other reservoirs, the total could approach 400,000 fish for the stretch of the Snake River between Lower Granite and Ice Harbor Dams.

During a low-flow year with no spill over the dams, the entire seaward migration of juvenile chinook salmon must pass through turbines. Although direct mortality through turbines is less than 15 percent at each dam (Schoeneman *et al.*, 1961), many fish are crippled or stunned and vulnerable to predators (Long and Krcma, 1969). Four hundred thousand squawfish could easily consume a significant fraction of the four to five million chinook salmon juveniles annually migrating down the Snake River under these conditions. This event may have occurred in the low-flow year of 1973 when Raymond (1974) measured an 88 percent mortality between Little Goose Dam and Ice Harbor Dam.

During higher flow years, much of the seaward migration passes over the spill with minimum mortality and stunning (Schoeneman *et al.*, 1961). Moreover, those passing through turbines are provided the additional protection of turbulence and high turbidity. In the high flow years of 1971 and 1974, only a 50 percent mortality was measured between Little Goose and Ice Harbor Dams, largely the result of prolonged exposure to high levels of TDG saturation instead of predation (Raymond, 1974). Spillway deflectors, installed at Lower Granite and Lower Monumental Dams in 1975 to reduce gas saturation, reduced mortality to 33 percent between Lower Granite and Ice Harbor Dams (Ebel and Raymond, 1976).

#### Conclusions

Based on laboratory studies in shallow tanks (0.25 m in depth), adult northern squawfish were severely affected—high mortality, physical impairment, and decreased ability to feed—when exposed to TDG concentrations 117 percent of saturation and above.

Field studies generally corroborated findings in the laboratory. However, below the tailrace of the dams, we found that most squawfish resided at depths below 3 m where they would be equilibrated to high gas saturation and could make quick foraging trips to the surface and back to depth without any serious gas problems. This finding indicated that predation during high concentrations of supersaturation may be even greater than expected.

Continued assessment of squawfish abundance, food consumption, and distribution

under different levels of TDG saturation is needed to measure accurately the effect on the survival of juvenile salmon and steelhead trout.

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# Some Effects of Simultaneous Thermal and Exercise Stress in Rainbow Trout (Salmo gairdneri)

**Abstract**

The combined effects of sublethal heat stress and enforced swimming on blood parameters were investigated in rainbow trout (*Salmo gairdneri*). Trout acclimated to 12°C were exposed to 12°, 17° (ΔT 5°C), 22° (ΔT 10°), and 27°C (ΔT 15°C) while resting or swimming at cruising speed. Plasma glucose and lactate were measured after 30 min each of rest and exercise. A temperature effect on plasma glucose level was apparent at 27°C, but not at 12°, 17°, or 22°C. Lactate level showed a similar pattern, with significant elevation only at 27°C. Plasma glucose and lactate were significantly higher in exercised than in rested fish at 12° and 22°C, but not at 17° or 27°C. An interaction between exercise and temperature was reflected in trout swimming performance.

## Introduction

Intake and discharge of large volumes of cooling water at power generating stations create strong local currents. Rejected heat simultaneously raises water temperatures. Although swimming against currents or encountering thermal changes are normal for most fish, the abruptness and magnitude of current and temperature gradients near power stations may impose stress. Increased temperature and swimming effort generally stimulate oxygen consumption in fish (Rao, 1968; Heath and Hughes, 1973), and an excessive increase in either can ultimately be fatal (Black, 1958).

Metabolic requirements of exercise have been extensively studied in salmonids (Black *et al.*, 1961). When fish swim at cruising speed, energy requirements are met by aerobic mechanisms. Greater swimming effort activates anaerobic energy production and elevates plasma lactate (Driedzic and Kiceniuk, 1976). Many fish species, subjected to acute sublethal heat stress, show a rapid elevation of plasma glucose (Schneider *et al.*, 1975; Wedemeyer, 1973). Hyperglycemia is hormonally mediated (Nakano and Tomlinson, 1967), and it is a sensitive indicator of environmental stress (Silbergeld, 1974).

Fry and Hart (1948) studied temperature effects on cruising speed of goldfish. More recently, Brett (1967) and Griffiths and Alderdice (1972) observed temperature effects on critical swim speed of salmon, especially at elevated temperatures in the zone of thermal resistance. Temperature effects on critical swim speed were also

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determined in three species of warm water fishes (Hocutt, 1973) and perch (Otto and O'Hara-Rice, 1974). Kutty and Sukumaran (1975) studied the ability of a cichlid to swim continuosly at fixed velocity while temperature was increased above the lethal level.

We evaluated combined effects of acute heat stress and enforced swimming on rainbow trout (*Salmo gairdneri*). The experimental design was a 4 x 2 factorial experiment with four test temperatures: 12°, 17°, 22°, and 27°C; and two treatments: rested (no swimming) and exercised (swimming). Exercised fish were forced to swim at cruising speed (2.5 body lengths/sec) for a fixed time period or until unable to perform. Plasma glucose and lactate measurements were used to evaluate extent of stress imposed by experimental conditions.

**Methods**

Two-year-old (25.5 cm mean standard length) rainbow trout were raised from stocks maintained under controlled conditions in our laboratories. Trout were fed commercial dry pellets daily and were held in filtered flowing Columbia River water at ambient temperature. Five weeks before testing, fish were moved to a 1.2 m circular fiberglass tank and temperature was adjusted 1°C per day to reach 12°C acclimation. Temperature was manually controlled within $\pm$ 0.5°C of the desired temperature. Two weeks before testing began, fish were moved to a trap tank (Schneider *et al.*, 1977) that permitted serial removal of individual fish without stressing the remaining stock. Water temperature in the trap tank was controlled to 12°C $\pm$ 0.1°C.

Exercise was induced in a revolving annular ring (Fry and Hart, 1948). The inner and outer ring walls formed an exercise channel 19 cm wide by 15 cm deep. The ring floated in a water bath and was positioned by three casters. A DC motor and friction drive wheel against the outer wall rotated the ring at desired speeds. Water velocity in the ring was measured by a hot film anemometer, Thermal Systems Inc., Model 1051-B®. An electrified barrier across the ring channel stimulated swim performance. Fish that touched the barrier received an electric shock discharged from a 0.47 $\mu$F condenser. Preliminary experiments showed that the charge stimulated swimming, but did not influence the blood chemistry parameters.

The experimental apparatus included a chamber which permitted holding one fish quiescent while a second fish was simultaneously undergoing forced exercise. The resting chamber was baffled to minimize incoming water currents. A plastic mesh basket in the resting chamber restrained fish and permitted their quick removal at test termination.

Water flow to the exercise ring and resting chamber was supplied at 8-10 $\ell$/min and was temperature-controlled to $\pm$ 0.5°C of the test temperature. The annular ring and resting chamber each received about half the supply flow. Dissolved oxygen in supply water was maintained at 100 percent of saturation with a Genoway bubble tray (Dean, 1973). Temperature in the exercise unit was monitored with a Hewlett-Packard quartz thermometer, Model 2801-A®.

To conduct each test, one trout was removed from the trap tank and placed in the stationary exercise ring; a second trout was immediately placed in the resting chamber. The experimental regimen was divided into two segments: a 30-min ad-

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justment period and a 30-min test period. During the adjustment period, water temperature and velocity were increased as required. Temperature was either held at 12°C or adjusted to 17°, 22°, or 27°C ± 0.2°C at the rate of 0.5°C/min. Water velocity was raised in small increments to the test velocity of 0.6 m/sec (2.5 body lengths/sec). The last velocity increase occurred 10 min prior to the test period, which permitted the fish to adjust to the velocity change (Webb, 1971). Each test was conducted with paired trout (i.e., one exercised and one rested); the test was terminated for each fish when it lost equilibrium, when an exercised fish failed to perform, or at the end of the 30-min test period.

Trout were observed during each test via an inclined mirror, and performance was monitored by an event recorder coupled to the electrified tail screen. Exhaustion was determined by loss of equilibrium or failure to respond to the electrical stimulus.

At test termination, trout were removed and immobilized in an alcohol-dry ice slurry. Blood (0.4-0.9 ml) was drawn from the dorsal aorta with a heparinized syringe (Schiffman, 1959). Plasma glucose was measured with a Beckman glucose analyzer.® Plasma lactate was measured by ultraviolet spectrophotometry using a Sigma Chemical Co. Kit, UV-826.® Fifteen control trout were removed from the trap tank and immobilized, and their blood was analyzed to establish glucose and lactate levels for fish experiencing minimum handling. Data for exercised, rested, and control groups were compared by a t-test (Ostle and Mensing, 1975). Significance was determined at the 0.05 percent probability level.

#### Results

All trout completed the exercise regimen except those exposed to 27°C water. Rested fish held at 27°C had a mean test time of 29.5 ± 0.36 (mean and standard error of the mean) min, which represents 98.3 percent of the 30-min test period. Two of the nine rested fish lost equilibrium just prior to the end of the test period. However, mean test time for this group was not significantly different from that of the other test temperature groups. Exercised trout subjected to 27°C swam only 8.8 ± 3.8 min (29.3 percent of the test period). Performance was significantly different from that of other exercised groups.

When rotation of the exercise ring began, trout displayed positive rheotaxis and moved upstream behind the tail screen; they usually remained there for the duration of the test, swimming apparently effortlessly. Fatigued fish showed characteristic changes in swimming behavior, marked by episodes of drifting "downstream," and into the tail screen. One or two shocks from the electrified barrier were generally enough to induce swimming from the tail screen area.

Fatigued trout became discolored and gills became engorged and distended with blood. Fish also had difficulty holding position in relation to current; their swimming became progressively more erratic. Side-to-side body movements became pronounced, and there was increased drifting to the tail screen. Fish braced their tails against the screen to remain upright. Initially electrical shocks stimulated movement from the screen, but subsequent encounters became more frequent. Eventually fish either lost equilibrium, or were pinned to the tail screen. At this point the test was terminated. There was a significant difference in plasma glucose level (Fig. 1) between control and rested trout tested at 12°C. However, there was no significant difference in plasma lactate of these two groups (Fig. 2).

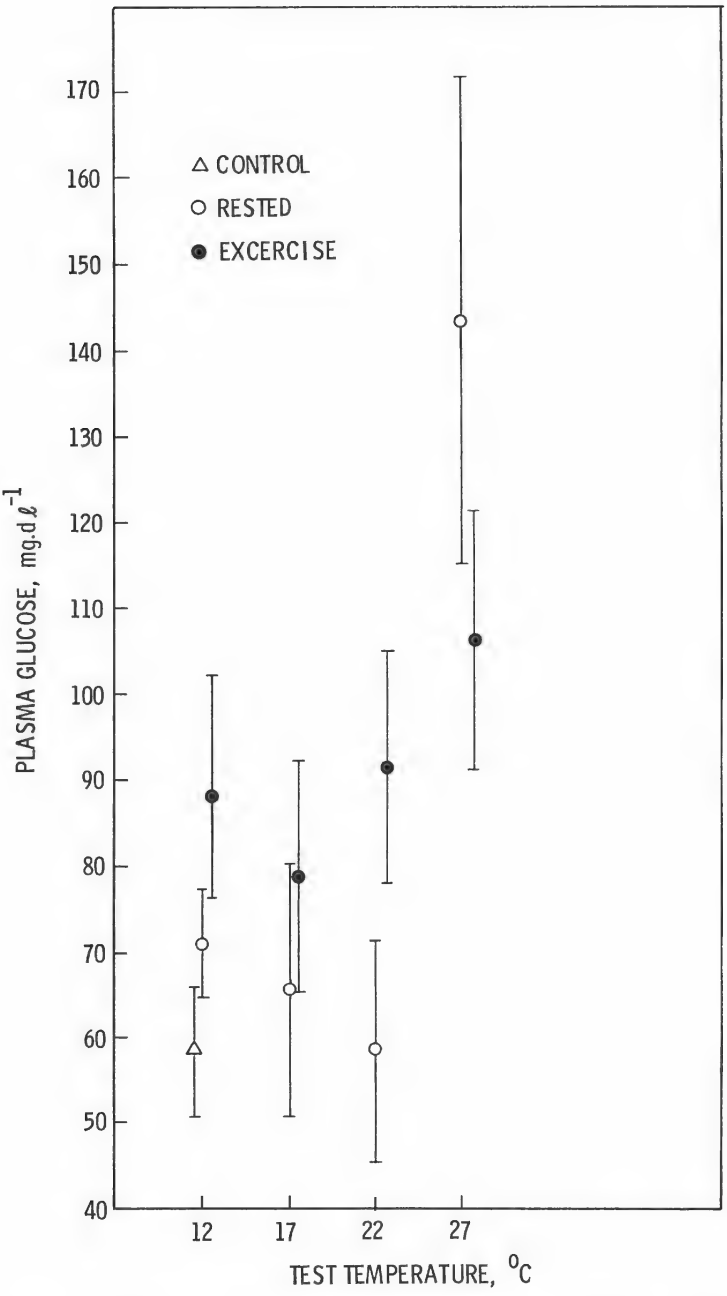


Figure 1. Plasma glucose (means and 95 percent confidence intervals) of control, rested, and exercised rainbow trout at 12°, 17°, 22°, and 27°C.

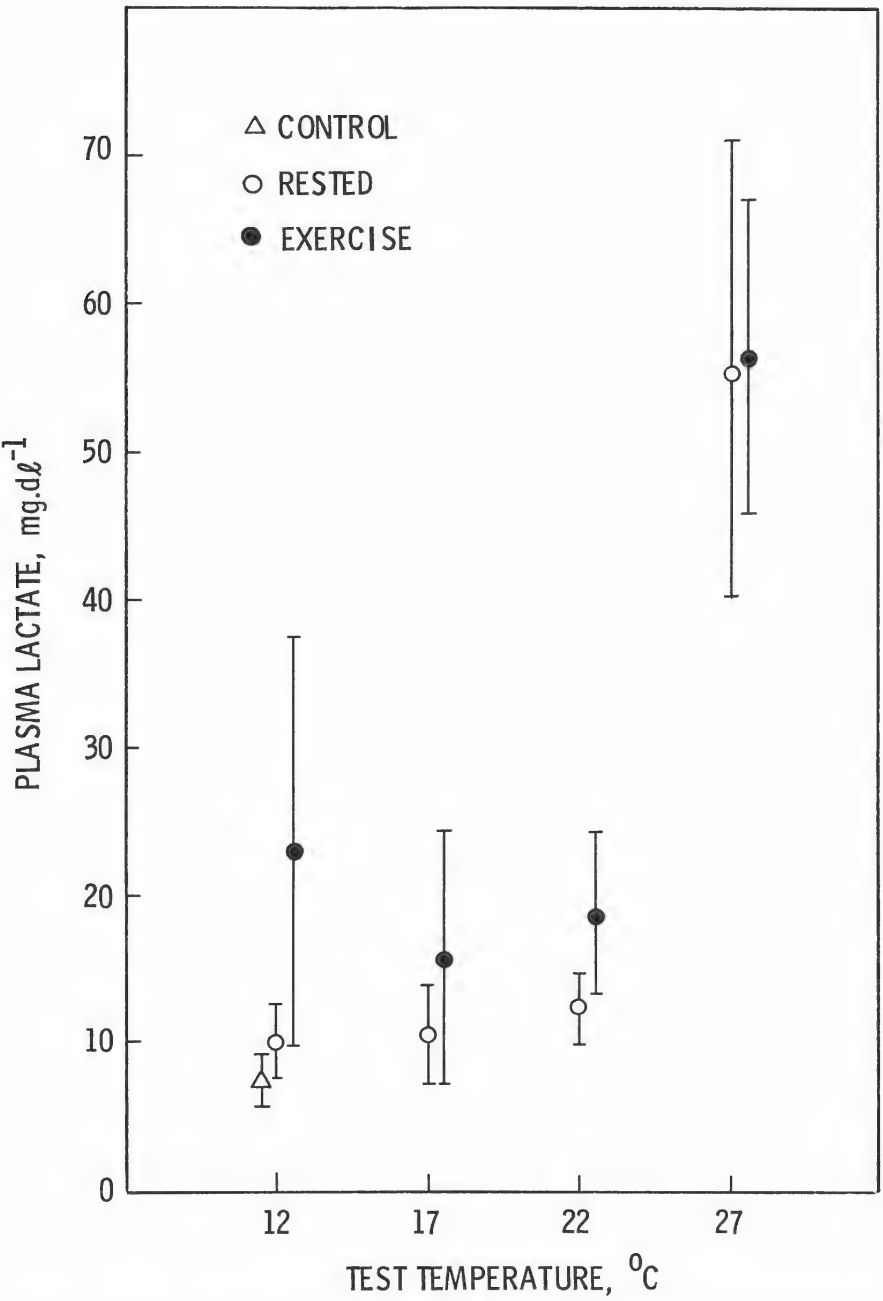


Figure 2. Plasma lactate (means and 95 percent confidence intervals) of control, rested, and exercised rainbow trout at 12°, 17°, 22°, and 27°C.

There were also significant differences between plasma glucose levels of rested and exercised fish at 12°, 22°, and 27°C but not at 17°C (Fig. 1). The plasma glucose level of rested fish was significantly higher at 27°C than at 12°, 17°, or 22°C. In exercised fish, significantly higher plasma glucose was detected at 27°C than that in fish tested at either 12° or 17°C. There were no significant differences between groups tested at 12° and 17°C or at 22°C and 27°C.

Comparison of plasma glucose lactate between rested and exercised fish showed a significant difference at 12° and 22°C but not at 17° or 27°C (Fig. 2). Temperature significantly affected plasma lactate only at 27°C.

**Discussion**

Several criteria have been used to evaluate swimming performance of fish, including critical swim speed (Hocutt, 1973; Webb, 1971), burst speed (Bainbridge, 1961), incremental velocity changes until fatigue (Driedzic and Kiceniuk, 1976), and effects of physical harrassment (Black *et al.*, 1961; Dean and Goodnight, 1964). Each technique has its merits. Our objective was to assess effects of thermal stress on sustained swimming ability of rainbow trout in simulation of physical events expected in thermal discharges of power plants (Spigarelli, 1975). We selected a sustained swim speed within the normal cruising range of rainbow trout (Blaxter, 1969; Bainbridge, 1961; Webb, 1971) for the exercise phase of our experiments.

Plasma glucose and lactate levels of our controls compared favorably with values reported for rainbow trout by Black *et al.* (1961). Fish were captured and transferred to the exercise ring with minimum stimulation and struggling. However, some handling stress was manifested by elevated plasma glucose in the 12°C rested fish compared to control fish.

Our results showed that 12°C acclimated rainbow trout could perform at temperatures up to 22°C. At 27°C ($\triangle$T 15°C), near the upper incipient lethal temperature (Charlon *et al.*, 1970), rainbow trout failed to sustain swimming for 30 min. However, seven of nine resting fish maintained equilibrium through the test period. Brett (1967) examined activity of young sockeye salmon (*Oncorhynchus nerka*) at high temperature and found a rapid decline in sustained swimming ability above the lethal temperature zone. Kutty and Sukumaran (1975) observed a decrease in the upper critical temperature of the cichlid *Tilapia mossambica* with increased activity and concluded that temperature and activity were interacting.

Elevated glucose and lactate indicated that 12° and 22°C produced stress in rainbow trout swimming at cruising speed. This finding is consistent with earlier investigations (Wedemeyer, 1973; Hudson, 1973; Walker and Pull, 1973). Fish swimming at cruising speed may rely solely on red muscle fibers for mobility (Driedzic and Kiceniuk, 1976). Thus, lactate usually produced by white muscle involvement would not be elevated by swimming conditions in our test design. However, Smit *et al.* (1971) concluded that both red and white muscle fibers are active at sustained swimming speeds. Our results support this latter conclusion.

Plasma glucose and lactate were similar at 17°C for rested and exercised fish. The apparent absence of stress may reflect the relationship of this test temperature to acclimation temperature. Javaid and Anderson (1967) determined that 10° and 15°C acclimated trout selected water temperatures of 15°-17°C and 17°-19°C, respectively, in a thermal gradient. Our tests at 17°C may reflect an attenuation of the combined

temperature and exercise stresses manifested in similar glucose and lactate levels in rested and exercised fish.

At 27°C ($\triangle$T 15°C), glucose levels of exercised trout were significantly lower than in rested trout (Fig. 1), and exercised trout failed to sustain swimming for the 30-min test period. Exercised fish swam only 29.3 percent of the test period. Thus, time may have been insufficient to mobilize stored liver glycogen to produce hyperglycemia.

Stress induced by elevated temperature was not apparent within the zone of thermal tolerance for rainbow trout; i.e., the levels of plasma glucose and lactate were comparable at 12°, 17°, and 22°C. When the test temperature was 27°C, plasma glucose and lactate increased significantly, indicating thermally induced physiological stress. Similar observations were reported by Wedemeyer (1973) and Schneider *et al.* (1974).

Plasma lactate was significantly higher in both rested and exercised trout at 27°C ($\triangle$T 15°C) than at 12°, 17°, and 22°C. However, plasma lactate of rested and exercised fish was identical at 27°C, a point at which a difference might be expected. Each of the stresses, heat and exercise, can place severe metabolic demands on fish. Rapid swimming increases $0_2$ uptake tenfold (Fry, 1957). Oxygen consumption increases threefold when temperature increases 10°C (Heath and Hughes, 1973). Thus, fish in our study were stressed and aerobic metabolism was inadequate; anaerobic metabolism produced the elevated plasma lactate.

Possibly lactate levels in exercised trout were not higher than rested trout at 27°C because of their different test periods, as explained above. Peak lactate measurements following exercise in trout do not occur until 3-4 hr after cessation of swimming (Black *et al.*, 1966; Stevens and Black, 1966; Hammond and Hickman, 1966). The elevated plasma lactate we measured at 27°C may be a function only of thermal stress because sufficient time did not elapse to reveal lactate levels produced by exercise.

We have established a qualitative difference between rainbow trout subjected to a temperature increase and rainbow trout forced to sustain swimming activity at the higher temperatures. The interaction occurs at temperatures above 22°C. Our results further indicate that sustained swimming at 22°C ($\triangle$T = 10°C) produces measureable stress that is not produced by either factor acting alone.

**Acknowledgments**

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# Notes on the Biology of the Miller Lake Lamprey
## Lampetra (Entosphenus) minima[1]

**Abstract**

Biology and life history of the extinct Miller Lake lamprey were studied by examination of field notes and preserved specimens. The life span was approximately 36 months. About 30 months were spent in the larval stage, with metamorphosis to the adult stage in the fall and spawning in late spring and early summer. Although the adults fed voraciously on trout and chubs, and were involved in cannibalism and scavenging, the shrinkage in length from full-term larvae to spawning adults was about 4.5 percent. Speciation of this dwarf lamprey apparently required less than 6600 years, for fish life of Miller Lake is thought to have been destroyed by the explosion of Mount Mazama, only 38 km distant. Reduced food supply for lampreys reinvading the lake, relatively short generation time, and the "founder effect" are thought to have been involved in the rapid speciation.

### Introduction

*Lampetra* (*Entosphenus*) *minima* is a dwarfed parasitic lamprey formerly found only in Miller Lake, Klamath County, Oregon. Fish control operations during the 1950s caused the apparent extinction of this species (Bond and Kan, 1973). Subsequent intensive investigation of the lake and outlet stream by the Oregon Department of Fish and Wildlife has disclosed no specimens (Harry Lorz, ODFW, pers. comm.). The location of Miller Lake is T27S, R6 1/2E, Secs. 11-14, about 16 km northeast of Mt. Thielsen.

### Biology

Bond and Kan (1973) described and named *L. minima* and Kan (1975) discussed the species briefly. The objective of this paper is to examine the life history of *L. minima* and to relate the biology of the species to its apparently rapid rate of speciation. The biology of this species can be studied only in retrospect, based on preserved specimens mostly in the Fish Collection, Department of Fisheries and Wildlife, Oregon State University (OS), and notes and observations made in the early 1950s.

Unlike other parasitic species of lampreys, *L. minima* was considerably larger in total length in late larval stage and the feeding stage than in the spawning stage (Bond and Kan, 1973) (Fig. 1). Shrinkage from the feeding stage is about 13 per-

[1]Technical paper #5258, Oregon Agricultural Experiment Station.

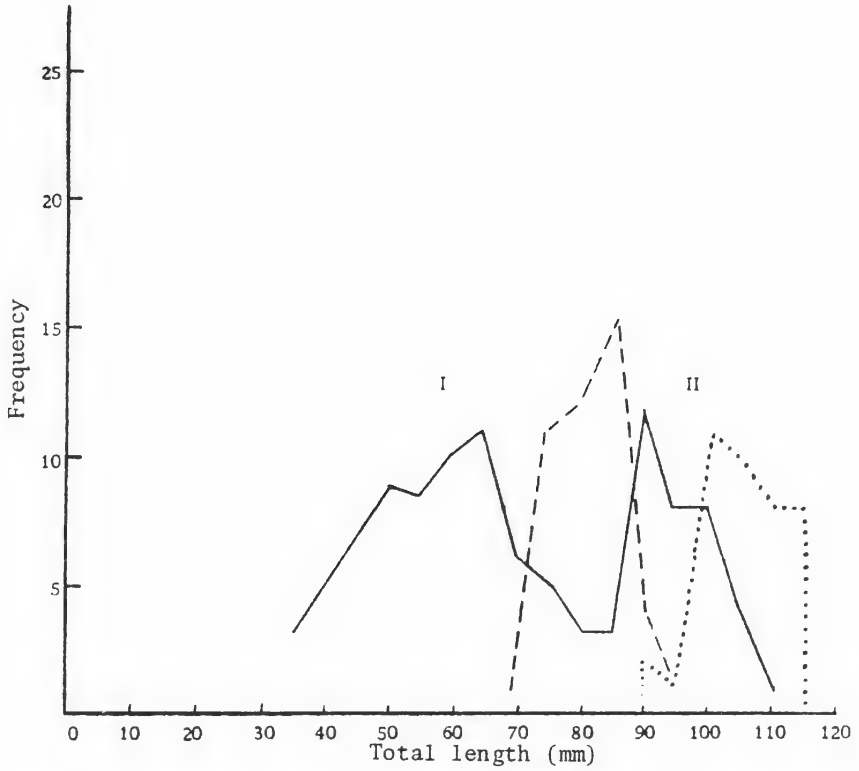


Figure 1. Length-frequency distribution for *Lampetra minima* ammocoetes (102 specimens, indicated by solid line), feeders (44, dotted line), and spawners (40, broken line) from Miller Lake, Oregon.

cent; spawners are about 4.5 percent smaller than the ammocoetes of age class II. Thus, the postlarval period of *minima* was shortened compared to landlocked *L. tridentata* of the Klamath Basin. *L. minima* metamorphosed in fall and spawned in June and July. The feeding period was therefore less than a year. During this short period, *L. minima* fed voraciously when prey animals were available. Lamprey marks were observed on tui chubs, *Gila bicolor*, and the planted fingerlings of brown trout, *Salmo trutta*, and brook trout, *Salvelinus fontinalis*. Cannibalism (see Davis, 1967) also played a part in the nutrition of *minima*, for scars and mined-out holes were found on specimens in collections of *minima* at feeding stage (OS 2811 and 2879). Scavenging was seen on several occasions. Dead tui chubs and lampreys were continuously attended by feeding lampreys until all soft material was removed. Chubs were sometimes reduced to a perforated skin surrounding the skeleton.

Egg counts for 10 *L. minima* range from 503 to 727, with a mean of 604.40. Relative fecundity (no. of eggs per g of egg mass/total body weight in g) varies from

432 to 596 (mean 525). Compared with other lampreys as listed by Hardisty (1971), the absolute fecundity of *minima* is the lowest, apparently a consequence of its extremely small adult size. On the other hand, the relative fecundity of *minima* is among the highest, indicating that a large fraction of the lipid reserves accumulated during larval life and the short parasitic period would be incorporated into gonadal products so that little reserve would be left for a spawning migration up tributaries. *L. minima* apparently had reduced the migration considerably; all spawners in the OS collection were collected along the lake shore. Few ammocoetes were collected from the cold tributary streams, but ammocoetes were common in deposits of organic detritus along the lake shore. Presumably ammocoetes were present in organic deposits in deeper water, but we have no collections from deeper than about 1 m.

Length-frequency distribution of 102 ammocoetes, most of which were collected in the fall along the lake shore, indicates the larval period of *L. minima* to be about 30 months (Fig. 1). By comparison, this duration is at least one year shorter than the larval period of *L. tridentata*, of which *minima* is a derivative (Kan, 1975).

#### Evolution

The evolution of *L. minima* apparently took place in the Miller Lake drainage following disruption of its connection with the remainder of the Klamath Lake drainage. The great Mount Mazama exploded about 6600 years ago (Powers and Wilcox, 1964), with thick fall of ash and pumice covering the surrounding area including the present Miller Lake district (Williams, 1942). The forerunner of *minima* must have survived the ashfall in the outlet stream or connecting waters (less likely in Miller Lake itself), but it seems probable that there were severe and lasting effects upon spawning sites and on food supply, so that the numbers surviving must have been small. Our hypothesis requires that the ancestral species must have abandoned the outlet stream following reinvasions of, or population rebound in, Miller Lake. A possible reason could have been interruption of water flow during the period of arid climate that prevailed during the time about 8000 to 4000 years before the present (Hansen, 1947; Heusser, 1966).

The shoreline spawning habit may have resulted from limited suitable space in the small tributaries and to their cold temperatures. Studies of the sea lamprey, *Petromyzon marinus*, disclosed that peak spawning and successful hatching took place at temperatures of 15.6° to 21.1°C (Applegate, 1950; McCauley, 1963; Piavis, 1961).

The only other fish species thought to have survived in the system was the tui chub, *Gila bicolor*, which has heavy scales and, except in very young stages, is not easy prey for a small lamprey. Moreover, the lake and environs, smothered by cinders and pumice, probably could not support a large population of either chubs or lampreys. Lampreys are known to respond to diminished food supply by reducing the ultimate body size, but without changing the duration of the feeding stage (Hardisty and Huggins, 1973). Smith (1971) reported a 13 percent reduction in size of *Petromyzon marinus* in the Great Lakes from 1947 to 1970. This change was independent of the abundance of lampreys but reflected a general reduction in food supply. In response to the supposed severe paucity of food, *L. minima* evidently evolved through two seemingly contrasting processes: feeding fiercely on whatever was available, and maturing early and spawning even on a starvation diet. These two processes were

apparently operating in view of its eventual characteristic adult body size and its observed feeding habits such as predation, cannibalism, and scavenging. As a result, *L. minima* remained extremely dwarfed and maintained the short adult life even though introduction of other species provided abundant food. Only one of our preserved specimens, a 129 mm adult (OS 2873), appears to have spent more than a few weeks to a few months in active feeding. The impact of predation upon planted trout fingerlings led to the destruction of the species through chemical control measurements during the 1950s.

### Speciation Rate

The speciation of *L. minima* must have required less than 6600 years. Factors that interacted with genetic processes and played an important role in bringing about this rapid rate include geographical isolation and severe ecological conditions, in particular reduced food supply.

Roles of geographical isolation in the process of gradual speciation have long been a subject of discussion. Mayr (1963) accumulated much evidence indicating that the process of speciation requires geographical isolation, the allopatric model of speciation. *L. minima* appeared to become geographically isolated from a probable landlocked *L. tridentata* type ancestry following the impact of the Mazama volcanism and arid climate. Duration of the isolation, some 6600 years, would seem insufficient to allow for the differentiation of a form to a full species level (see Hubbs, 1940; Miller, 1961); but during this period, *L. minima* accumulated distinctive characters including dwarfism, altered feeding habits, and partial or complete elimination of adfluvial migration, as well as reduced disc size, reduced dentition, and other salient characters (Bond and Kan, 1973).

No doubt the physiochemical makeup of the water in Miller Lake was greatly altered through addition of a large amount of hot volcanic ash and cinders generated by the Mazama eruption only 38 km away. Native fishes, including the lamprey, probably died out because of the sudden drastic environmental changes. Altered ecological conditions that confronted the reinvading or surviving fishes in the Miller Lake system must have played an important part in speciation.

After a sudden drastic environmental change has reduced a species to a very small population, the genotype of a majority has already been proven unsuccessful to meet the changed environment. The remnant of the now decimated species is faced with perishing or adapting. Adaptation can be facilitated through inbreeding in a small population. Population size of the incipient *L. minima* in Miller Lake was apparently very small because of the impact of the Mazama ashfall. By comparison with the supposed parent species, *L. tridentata*, some characteristics of *L. minima* including the dentition and adult body size are remarkably constant (Kan, 1975), suggesting that inbreeding in a small population had indeed occurred.

A short generation time appears to favor a rapid speciation rate in isolated freshwater fishes (Miller, 1961). The three-year generation of *minima* was longer than the generation time of most freshwater teleosts, but was short for a lamprey; this fact may have speeded the rate of speciation.

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Fred Locke kindly supplied field notes, specimens, and other information. James D. Hall and Robert L. Jarvis critically read the manuscript.

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# **Foods of Oregon Silver-Haired Bats,** Lasionycteris noctivagans

**Abstract**

The silver-haired bat in Oregon feeds on a variety of insects. Major items are Lepidoptera, Homoptera (primarily Cercopidae), Hemiptera, Hymenoptera (primarily Formicidae), Coleoptera, and Neuroptera (Hemerobiidae).

## Introduction

Little information exists on the food habits of silver-haired bats, *Lasionycteris noctivagans.* Gould (1955) found a stable fly, *Stomoxys calcitrans*, in the mouth of an individual from Massachusetts; Novakowski (1956) found young silver-haired bats feeding on dipterous larvae in an abandoned woodpecker hole in which they lived. Whitaker (1972) found 100 percent Trichoptera in the stomach of one and 90 percent Trichoptera and 10 percent Scarabaeidae in the stomach of another silver-haired bat from Indiana. Whitaker *et al.* (1977) found that the major foods of silver-haired bats ($n = 15$) in western Oregon varied but included Lepidoptera (32.0 percent volume), Diptera (18.9 percent), Isoptera (14.0 percent), and Hymenoptera (7.0 percent).

The purpose of this paper is to present information on the food habits of silver-haired bats from eastern Oregon.

## Methods and Materials

Most bats were taken in Wallowa County in conjunction with DDT studies and in Grant County in conjunction with grazing studies. Some bats, however, were from Baker, Malheur, Harney, and Union Counties. The bats were captured in mist nets placed over waterholes.

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We have data from (41) stomachs and 124 scats (Table 1). Stomach contents were taken from sacrificed bats, and scats were collected by keeping bats overnight in suitable holding containers before releasing them.

TABLE 1. Food of silver-haired bats (**Lasionycteris noctivagans**) from eastern Oregon, based on stomach and scat analysis.

| | Stomachs (n = 41) | | Scats (n = 124) | |
|---|---|---|---|---|
| | % Volume | % Frequency | % Volume | % Frequency |
| Lepidoptera | | | | |
| Unidentified | 29.7 | 51.2 | 67.7 | 97.6 |
| Diptera | | | | |
| Unidentified | 10.9 | 39.0 | 9.6 | 44.4 |
| Tipulidae | — | — | 5.4 | 23.4 |
| Chironomidae | 0.05 | 2.4 | — | — |
| Muscoidea | — | — | 0.1 | 1.6 |
| Otitidae | — | — | 0.01 | 0.8 |
| Homoptera | | | | |
| Cercopidae | 22.7 | 43.9 | — | — |
| Cicadellidae | 1.7 | 14.6 | 0.7 | 0.8 |
| Fulgoridae | 0.1 | 2.4 | — | — |
| Unidentified | — | — | 0.8 | 4.0 |
| Hemiptera | | | | |
| Unidentified | 7.9 | 39.0 | 1.3 | 9.7 |
| Lygaeidae | — | — | 0.8 | 7.3 |
| Miridae | — | — | 0.3 | 1.6 |
| Coreidae | — | — | 0.1 | 0.8 |
| Hymenoptera | | | | |
| Formicidae | 12.2 | 31.7 | 0.5 | 5.6 |
| Unidentified | — | — | 0.2 | 0.8 |
| Coleoptera | | | | |
| Unidentified | 8.4 | 34.1 | 1.0 | 8.9 |
| Chrysomelidae | 1.2 | 4.9 | 0.1 | 0.8 |
| Scarabaeidae | 1.0 | 4.9 | 0.1 | 0.8 |
| Carabidae | 0.1 | 2.4 | 0.7 | 0.8 |
| Trichoptera | | | | |
| Unidentified | 1.1 | 2.4 | — | — |
| Orthoptera | | | | |
| Unidentified | — | — | 1.2 | 2.4 |
| Isoptera | | | | |
| Termitidae | — | — | 0.4 | 1.6 |
| Neuroptera | | | | |
| Hemerobiidae | 0.5 | 7.3 | 6.4 | 25.8 |
| Chrysopidae | — | — | 0.04 | 0.8 |
| Unidentified Insect | 2.4 | 17.1 | 1.4 | 8.1 |
| Vegetation | — | — | 1.1 | 2.4 |
| Spider | — | — | 0.04 | 0.8 |
| Unidentified Material | — | — | 0.2 | 2.4 |
| | 100.0 | | 100.2 | |

**Results and Discussion**

The most important food of silver-haired bats from eastern Oregon was adult Lepidoptera, forming only 29.7 percent of the volume in stomachs, but comprising 67.7 percent in scats (Table 1). Flies were also important in stomach and scat samples. Several foods important among the stomach samples, such as the froghoppers (Cercopidae, 22.7 percent volume), ants (Formicidae, 12.2 percent), and unidentified beetles (12.7 percent), were of relatively little importance in the scat samples. Besides moths, unidentified flies, Hemerobiidae, and Tipulidae were important in scats, but of little importance in stomachs. Thus, the foods varied between the two types of samples.

Three possible causes for these discrepancies are: (1) differential results related

to the examination of stomach vs. scat samples; (2) differential availability of prey items to the bats in the two samples; and (3) differential digestibility.

The use of stomach contents is generally superior to scats for food habits analysis because of the problem of differential digestion. Digestible items will be in constantly decreasing quantity as they move backward in the digestive tract. Flying insects, however, have chitinous hard parts which digest but little, and North American bats feed almost entirely on flying insects. Thus, scat analysis would seem to introduce less bias from differential digestion than would be the case with food habit studies of many other species. The use of the scat, rather than stomach, analysis is especially valuable because some species of bats are greatly decreasing in abundance.

All scat samples were from Grant County. Comparison of stomach and scat samples taken at the same time would allow comparison of the two techniques, but stomachs of only eight bats were available from the Grant County localities. Percent volumes of the main foods in these eight stomachs were Lepidoptera, 74.8 percent; unidentified Diptera, 14.4 percent; Cercopidae, 6.5 percent; Coleoptera, 2.5 percent; Cicadellidae, 1.3 percent; and Hemerobiidae, 0.6 percent. Lepidoptera and Diptera were similar in both scat and stomach samples. A more extensive comparison of stomachs versus scats is, however, in progress on other species of eastern Oregon bats.

The six main categories of foods in silver-haired bats from western and eastern Oregon, respectively, with percent volumes, were: moths (32.0, 29.7), flies (18.9, 11.0), termites (14.0, ——), bees and wasps (7.0, ——), hemipterans (6.6, 7.9), crickets (3.8, ——), Homoptera, mainly Cercopidae (——, 24.5), ants (——, 12.2), and beetles (——, 10.7).

Thus moths were the main food, forming just under a third of the volume in both cases, and flies and hemipterans were also important in stomachs and scats. The other three most important foods in the western Oregon sample, termites, bees and wasps, and crickets, did not occur, however, in stomachs from eastern Oregon bats. The remaining three most important foods of eastern Oregon silver-haired bats were cercopids, ants, and beetles. All three occurred at low rates in western Oregon stomachs. We know of no good reasons for these differences in food habits, other than differential availability of prey. This hypothesis may not, however, be the entire answer.

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# Distribution and Relationship of Mountain Beaver to Openings in Sapling Stands

## Abstract

Observations in sapling stands of unthinned Douglas-fir (*Pseudotsuga menziesii*) showed that mountain beaver (*Aplodontia rufa*) are usually associated with the treeless openings. Vegetation found in these openings provides the majority of their food and nesting material. Mountain beaver damage to saplings usually occurs in the border areas around these openings. The levels of damage appear related to stand characteristics such as age, size, and density of trees and to the degree of canopy closure. In this study, the heaviest damage by mountain beaver occurred to trees nine to twelve years old and coincided with the approximate time of canopy closure. The distribution of animals, their use of vegetation, and the patterns of damage suggest that as the tree canopy closes, understory vegetation is suppressed and damage levels increase as mountain beaver are then forced to rely on Douglas-fir for food. Slab and increment core samples provide an effective means of dating damage.

## Introduction

Mountain beaver (*Aplodontia rufa*) damage saplings of Douglas-fir (*Pseudotsuga menziesii*) and other species in the 10- to 25-year age class, sometimes causing serious stocking reductions and economic losses. Basal girdling and undermining of roots are the most serious injuries inflicted on saplings (Hooven, 1977; Lawrence *et al.*, 1961). Observations reported in this paper suggest characteristics of mountain beaver distribution and their habitat use which may aid in understanding the problem and in controlling damage.

## Study Areas

Two representative areas were selected in the Clemons Tree Farm of Grays Harbor County, Washington; the Sylvia Creek unit located 6.4 km (4 mi) northwest of Montesano is 8.1 ha (20 a) in area, and the Satsop unit is 11.7 ha (28.9 a) and located 13.7 km (8.5 mi) northwest of Satsop.

The topography of the two units ranges from flat to gently rolling, with maximum slopes of 50 to 55 percent. Both areas are low elevation sites (less than 160 m), with soils in the Impie Series—moderately deep, granular silt loams which have a high site index (II+) for growth of Douglas-fir (Steinbrenner and Duncan, 1969).

Both study units and the surrounding stands were logged in the early 1950s and regenerated by aerial and natural seeding about 1957. Prior to thinning, there were 2160 and 2346 stems per hectare (875 and 950 stems per acre) in the Sylvia Creek and Satsop

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units, respectively. Douglas-fir was the predominant species (over 94 percent) with some western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and western red cedar (*Thuja plicata*) present. In both units, average DBH was 102 mm (4.0 in.) and average age was 18 years. The principal understory vegetation was sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*). Both stands were interspersed with mixed hardwood thickets, consisting mostly of alder (*Alnus rubra*) and cascara (*Rhamnus purshiana*).

#### Procedures and Methods

Mountain beavers were captured in welded-wire live-traps placed in burrows exhibiting recent use by the animals; traps were set four consecutive nights each month from June to November 1976. All animals were marked with numbered metal tags placed in both ears when first captured, and sex, age, and location of capture for each animal were recorded. Animals were released where caught. Data were used to determine population size, activity patterns, movement, and home-range size. A modified inclusive boundary strip method (Blair, 1940) was used to determine the home range of mountain beavers captured three or more times.

Five mountain beavers also were instrumented with small, collar-type radio transmitters. Transmitter circuitry and methodology were similar to that described by Dodge and Church (1965) and Martin (1971). Two permanent monitoring stations were established near each burrow system in which signal refraction and interference were minimal. Using a portable receiver, animal locations were detected by triangulating two azimuth readings from the permanent monitoring stations, or by "homing in" on the signal intensity. Location readings were taken at least once a week from August to November 1976 at various times of the day for an average of 28 readings per mountain beaver. Telemetry data also were used to determine home ranges.

Vegetation, tree damage, and stocking levels were examined on 40.5 $m^2$ (435 $ft^2$) plots located on a 20-m by 40-m (66-ft by 132-ft) grid; Daubenmire's (1959) procedure for determining cover-class was used to estimate frequency of occurrence and density of vegetation. Trees were considered damaged if they exhibited signs of mountain beaver girdling or undermining.

In both sites, stem-maps were drawn of the areas around nine randomly selected openings used by mountain beavers. Slash, burrow openings, exposed runways, and stem locations were mapped, and all trees were measured (DBH) and assessed for damage.

Burrow entrances and tunnel food caches were sampled twice monthly to estimate the type of vegetation used by mountain beavers for food or nesting (Allen, 1969; Scheffer, 1929).

Slabs and increment cores were taken from randomly selected trees that showed mountain beaver feeding scars. For trees considered to be dominant or "leave" trees, two cores were taken at not more than 15 cm (6 in.) aboveground. These samples were taken at (1) the point of damage, and (2) an undamaged point at the same height. Slab samples were taken through the damaged section of other trees, at the same height as the core samples, and were stained with a 1 percent solution of Bismark Brown. Growth rings were counted and location of damage determined. The basal diameter at the time of damage was determined by measuring from the center of the slab to the

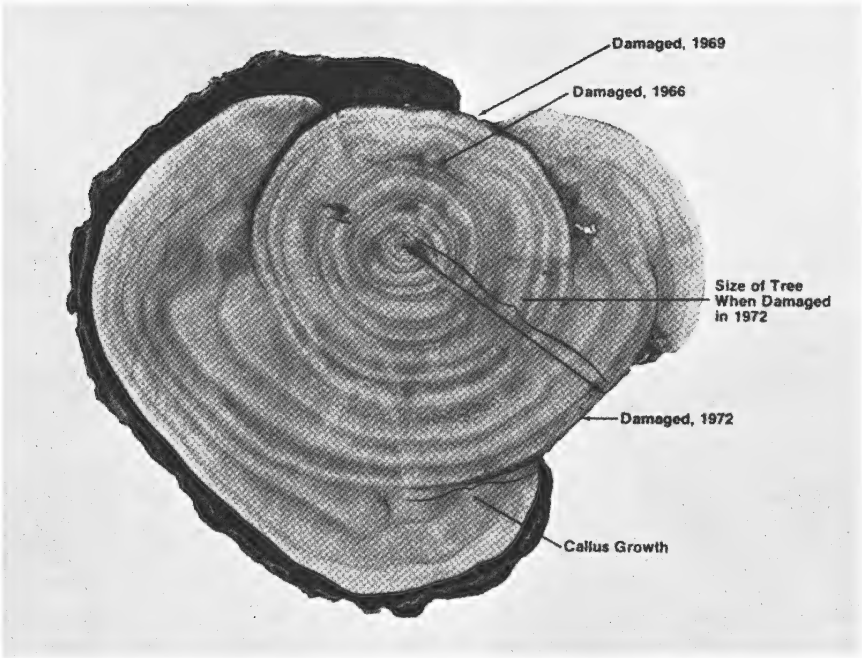


Figure 1. A slab sample showing multiple incidences of mountain beaver girdling and the procedure for determining the diameter class of the tree at each occurrence of injury.

furthest point of damaged wood (Fig. 1). Tree age and year when damage occurred were determined from the core samples.

#### Results and Discussion

Data from live-trapping indicate population levels of 40 mountain beaver in the Satsop unit and 29 in the Sylvia Creek unit. These estimates equal 3.4 and 3.6 animals per hectare (1.4 and 1.5 per acre), respectively, which are lower than population estimates based on operational trapping for damage control (6 to 7 mountain beaver per hectare, according to an unpublished Weyerhaeuser Company report, 1977).

Average home ranges of 16 of the 40 animals at Satsop and 19 of the 29 animals at Sylvia Creek were calculated at 0.17 $\pm$0.02 ha and 0.10 $\pm$0.01 ha, respectively; Martin (1971) and Lovejoy (1972) reported home ranges of comparable size. All mountain beaver except two were associated with stand openings (Figs. 2 and 3).

Comparison of home-range size with the proportion of the home range lacking tree cover (openings) produced a linear relationship. The greater the percent of opening in the home range, the smaller the home range. Clearings larger than 0.13 ha (0.32 a) were generally used by more than one mountain beaver. Many of the burrow runways which occurred in openings also were used by more than one mountain beaver, and overlapping home ranges were common. Martin (1971) and Lovejoy (1972) also observed common use of burrows in young plantations and sapling stands of mixed age. Openings smaller than 0.13 ha were generally used by a single individual; several small

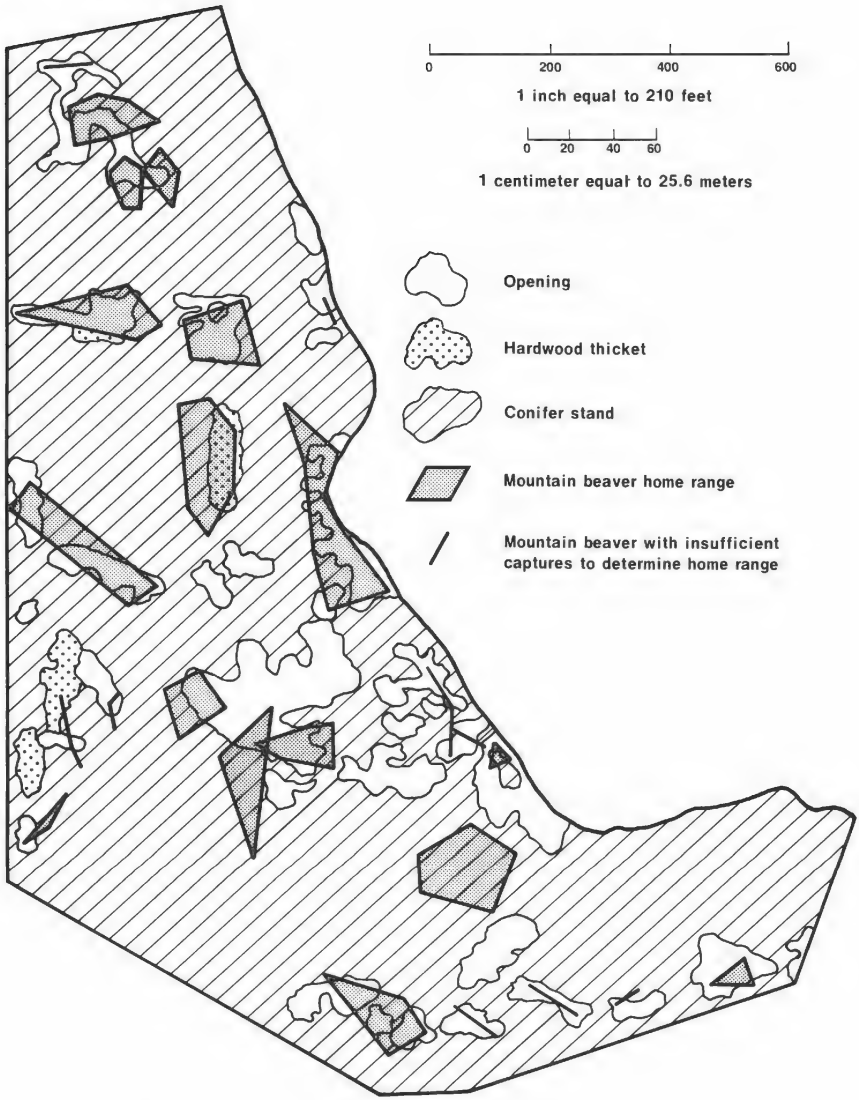


Figure 2. The relationship of mountain beaver in the Satsop study unit to openings in the stand.

openings may occur within a home range (Figs. 2 and 3). This association of home range to opening size suggests that openings are an important component of mountain beaver habitat in sapling stands.

Although openings are important, in only one case did the home range of a mountain beaver occur entirely within an opening. Home ranges usually extended from an opening into the stand, and included three major areas with distinct characteristics:

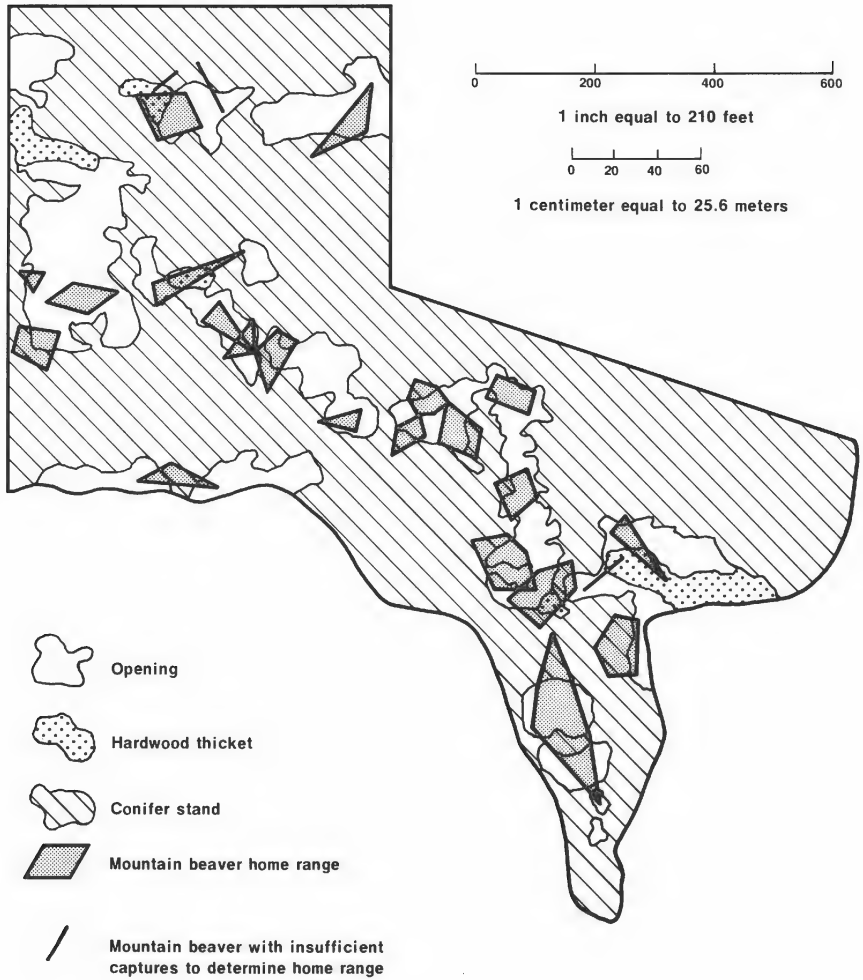
0 200 400 600
1 inch equal to 210 feet
0 20 40 60
1 centimeter equal to 25.6 meters
Opening
Hardwood thicket
Conifer stand
Mountain beaver home range
Mountain beaver with insufficient captures to determine home range

Figure 3. The relationship of mountain beaver in the Sylvia Creek unit to openings in the stand.

opening, stand, and border area. Herbaceous vegetation, principally grasses, bracken fern (*Pteridium aquilinum*), and forbs, characterized the openings; it was the type of vegetation most frequently found cached at burrow entrances during late spring and summer. Vegetation in the border areas, where the nest and the center of activity usually occurred, was primarily salal and sword fern. Under the closed canopy of the stands, salal and sword fern were sparse and bare ground predominated. Salal and sword fern were clipped year round, but the intensity of their use by mountain beavers increased after the fall die-off of grasses and forbs. Allen (1969) and Voth (1968) studied the food habits of mountain beavers and they reported similar uses of, and seasonal preference for, various plants.

Although the vegetative composition was similar for the two locations, the quantities of salal and herbaceous vegetation were greater at Sylvia Creek. This difference was probably a result of the more open nature of the stand at Sylvia Creek; 29 percent of the area was in openings, as compared with 16 percent in the Satsop unit. The greater abundance of herbaceous and shrubby vegetation reduces the need for mountain beaver to rely on trees for food, which may explain the greater incidence of damage to saplings in the Satsop unit.

Damage levels prior to thinning were only 19 percent of the trees in the Satsop unit and 3.5 percent in the Sylvia Creek unit. Precommercial thinning of these stands will reduce stocking about 50 percent and could remove many of the injured trees. However, mountain beaver damage usually occurs in the border around openings and continued tree killing could result in maintenance or expansion of these openings.

Slab and increment core samples taken from injured trees showed that most of the damage had occurred in 1972 (Fig. 4) to trees 9 to 12 years old (Fig. 5) and 50- to 75-mm basal diameter (Fig. 6).

One might expect damage to decrease as basal diameter increases because of the difficulty of girdling thicker bark; indeed, this finding could explain the lower incidence of damage to the larger trees. However, we have observed girdling by mountain beavers on trees larger than those measured in this study. Couch (1925) and Herlocker (1950) reported that mountain beavers can girdle trees 305 mm (1 ft) in diameter. Mountain beavers also can sever (clip) stems up to 19 mm in diameter (Herlocker, 1950; Lawrence *et al.*, 1961). It is conceivable that younger trees with a basal diameter less than 25 mm could have been clipped and removed by mountain beavers prior to our observations, so that damage to smaller trees could have been greater than what analysis of slab samples indicated. However, the timing of canopy closure resulting in suppression of understory vegetation appears to have more influence on the occurrence of damage than tree size. Other investigators (Crown and Brett, 1975; Reukema, 1975) have shown that the approximate time of canopy closure for managed Douglas-fir stands is 9 to 12 years. The stands in the study units reached this age in 1971-1973, which were also the years when the most damage occurred.

#### Management Implications

Observations in unthinned sapling stands composed predominantly of Douglas-fir show that mountain beavers are most often associated with openings. Home range characteristics and use of vegetation suggest that openings are an important part of mountain beaver habitat, providing the majority of herbaceous and shrubby vegetation used as food and nesting material.

Tree damage by mountain beavers appears related to the timing of stand closure and subsequent suppression of understory vegetation. This reduction in the quality of habitat for mountain beavers may force them to rely on Douglas-fir as a food source. Thinning at the time of stand closure may remove injured trees and help reduce the damage problem by opening the stand and allowing the development of herbaceous and shrubby vegetation. However, this event may simply delay the occurrence of damage until the thinned stand begins to close, at which time the impact may be greater due to the reduced levels of stocking.

The apparent reliance on openings suggests that eliminating these areas (a desir-

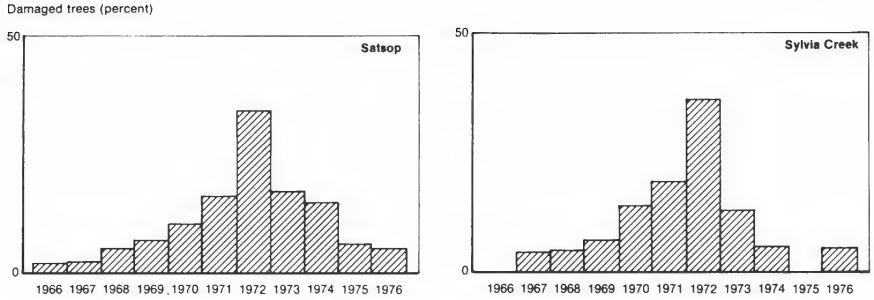


Figure 4. Incidence of mountain beaver injuries, by years, as revealed by analysis of stem sections from damaged trees.

Figure 5. Incidence of mountain beaver injuries related to tree age, as revealed by analysis of stem sections from damaged trees.

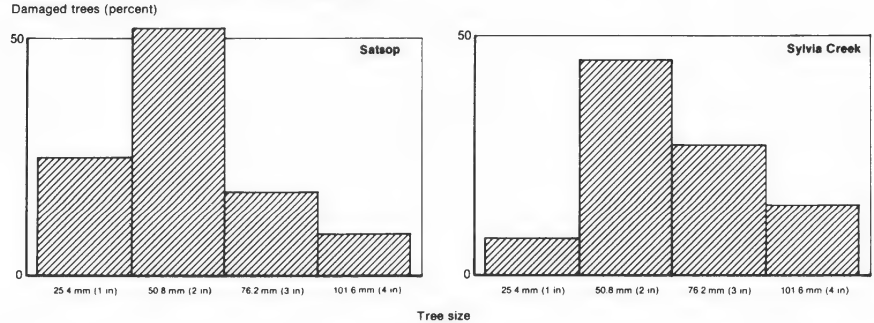
Damaged trees (percent)
50
0
Satsop
25.4 mm (1 in) 50.8 mm (2 in) 76.2 mm (3 in) 101.6 mm (4 in)
50
0
Sylvia Creek
25.4 mm (1 in) 50.8 mm (2 in) 76.2 mm (3 in) 101.6 mm (4 in)
Tree size

Figure 6. Incidence of mountain beaver injuries related to tree size (basal diameter), as revealed by analysis of stem sections from damaged trees.

able goal of forest management) would also reduce mountain beaver habitat and the potential for damage. Some openings are preventable, such as those resulting from accumulations of logging debris or piles of slash formed during site preparation. In addition to creating openings, the accumulations of debris provide good habitat for mountain beavers. The animals also are capable of producing and maintaining "holes" in the stand, especially in recently planted areas. Prevention of these types of openings should be accomplished early, during plantation establishment. Trapping mountain

beavers can effectively reduce animal numbers and damage; proper site preparation should reduce the amount of favorable habitat.

Treeless openings and poorly stocked areas in sapling stands occur from several causes, some of which are not preventable or easily corrected. In these cases, action should be directed at preventing further loss of trees and expansion of openings. Delaying thinning until trees are larger and favorable habitat is at a minimum may help reduce the damage potential, but yield reductions as a result of postponing thinning must be considered. Trapping or other direct control measures also can be used just prior to thinning operations. Particular emphasis in control efforts should be given to openings and border areas. One of the more promising approaches is chemical thinning: it releases the crop trees, but it leaves the treated trees in place and does not open the canopy and allow development of understory vegetation.

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# Lomatium: A Key Resource for Columbia Plateau Native Subsistence

**Abstract**

Ethnobiological research with contemporary Sahaptin-speaking Indians highlights the key role played by species of *Lomatium* (Umbelliferae) as sources of food energy and Vitamin C. Contemporary Sahaptin speakers' knowledge of *Lomatium* morphology and natural history reflects this contribution: 14 "folk species" recognized in native terminology correspond to 12 scientific species, at least 10 of which were eaten.

## Introduction

Analyses of the aboriginal foraging economies and their resource base in northwestern North America have stressed the abundance of the local fisheries nearly to the exclusion of the role of other available resources (Sneed, 1971; Hewes, 1973; Donald and Mitchell, 1975; Palmer, 1975a). These studies thus leave the impression that a male-dominated fishery was sufficient to provide for the population, and that the female economic contribution, primarily the harvest of vegetal foods, was non-essential. A long-standing bias in the anthropological literature is thus supported (Martin and Voorhies, 1975). We will argue that, for the interior plateau region of the middle Columbia River basin, the vegetable staples harvested by women were as important in native subsistence as the fish and game harvested by men. In support of this contention, we will demonstrate 1) the availability of these staples in sufficient quantity—taking into account native harvesting techniques—to meet the caloric needs of the estimated pre-contact population; and 2) the intensity of cultural interest directed by these peoples toward a single genus of plants, *Lomatium*, several species of which were staple elements or key supplements in the aboriginal diet.

It may be noted that, by contrast with native treatment, the lomatiums are infrequently and inconsistently named in English. There are no accepted common names for most of them, and such terms as "biscuit-root," "desert parsley," and "Indian celery" have been used for more than one species, making it easier for ethnographers to underestimate the number and importance of the plants the Indians recognize.

Indians for whom lomatiums were the primary vegetable resource occupied the Columbia River region from near The Dalles, Oregon, to Priest Rapids, Washington. Most of these Indians spoke a common language, known to linguists as Sahaptin, which

their descendants still speak on and around the Yakima, Warm Springs, and Umatilla Reservations (Rigsby, 1965). The Nez Perces, the Cayuse, the Chinookan-speaking Wasco and Wishram, and certain Salishan-speakers also relied on lomatiums as staples (Marshall, 1977; Turner, 1973; Turner, Bouchard, and Kennedy, 1980), but space precludes their consideration here. Following Rigsby (1965), we recognize 15 dialects of three major groups within the Sahaptin language: the Northwest dialect cluster includes Kittitas, Yakima, Upper Nisqually (extinct), Upper Cowlitz, and Klickitat; the Columbia River cluster includes Tenino, Tygh, Celilo, Rock Creek, John Day, and Umatilla; and the Northeast cluster includes Walla Walla, Snake River, Palouse, and Priest Rapids.[1] The Sahaptin life range may be defined as that region habitually traversed by Sahaptin-speakers in their annual food quest. Ethnographic reports indicate that this range consisted of a core of some 60,000 sq km clearly controlled by Sahaptin-speaking village groups and a peripheral area of some 50,000 sq km used jointly with people of adjacent language groups (Ray *et al.*, 1938; Spier, 1936; Indian Claims Commission, 1974). To calculate a density figure for the region, it is necessary to adjust for the sharing of resources with other groups in the peripheral area of the Sahaptin life range. We here assume that on average one-third of the resources of the peripheral portion of the range was available to Sahaptin speakers. Thus, the estimated pre-contact Sahaptin-speaking population of 14,500 (Mooney, 1928) had an overall density of about one person per 5 sq km. Such a density is considerably greater than that estimated for interior foraging groups immediately north and south of the Columbia Plateau (Kroeber, 1938).

This relatively dense population was supported by a rich anadromous fishery, a

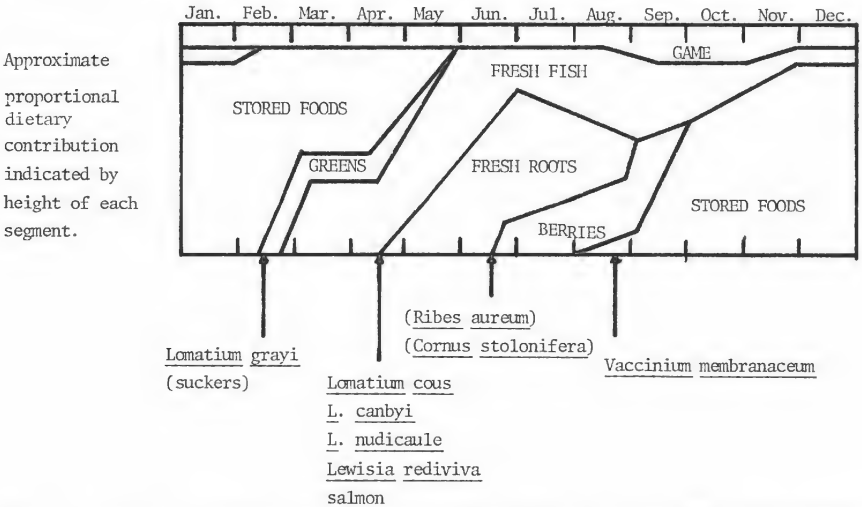


Figure 1. Schematic representation of seasonal patterns of food utilization by Sahaptin-speaking people of the middle Columbia Plateau. Species indicated below the diagram are those honored at first food feasts. Species in parentheses are feasted in a minority of contemporary communities.

[1]The orthography used here follows: obstruents, plain stops, and affricates / p, t, c, λ', č, k, $k^w$, q, $q^w$ /; glottalized stops and affricates / p', t', c', λ', č', k', $k^{w'}$, q', $q^{w'}$ /; and spirants / s, l, š, x, $x^w$, x̣, $x̣^w$ /, sonorants /m, n, l, w, y, /, laryngeals / h, ? /, and vowels / i, ii, ɨ, u, uu, a, aa / (Rigsby, n. d.).

"displaced piece of the Pacific Ocean," as it were, and by the systematic exploitation of vegetable products in season. The traditional economy was planned at the household level to take advantage of seasonal patterns of food availability. First food feasts, still celebrated today, ritually marked the key phases of this seasonal cycle, as illustrated schematically in Figure 1. One may recognize two major productive phases with respect to plant foods in this seasonal round, a "root"-digging phase and a "fruit"-picking phase. The "root" phase is marked by a minor feast at the onset and a major feast at the peak of root maturation. The "fruit" phase is ritually marked likewise. The Sahaptin classification of plant products also reflects this major seasonal division in the distinction between *x̣nít* 'foods which are dug,' including primarily roots harvested in spring, and *tmaanít* 'foods which are picked,' including primarily fruits harvested in fall. The latter are dominated by species of the genus *Vaccinium*, huckleberries and their relatives, of which at least six are nomenclaturally differentiated, while the former are dominated by *Lomatium* species, with 14 distinct folk taxa given recognition. The 10 lomatiums which were eaten represent nearly 30 percent of all Sahaptin edible root species.

The genus *Lomatium* has its greatest diversity in the Columbia Plateau area (Mathias, 1965). A typical edible *Lomatium* survives on scattered, barren patches of lithosol habitat by means of nutrients stored in a thickened root. The Indians call these lithosol patches *šám* and systematically utilize them as prime root digging sites.

Of the 29 *Lomatium* species known to occur in some part of the Sahaptin range, three have not yet been shown to Sahaptin speakers, and four others have not been shown to Sahaptin speakers familiar with the areas where the species are found. Ten others were clearly recognized as familiar but were not formally named. These 17 species are all rare, of very local occurrence, or marginal to the area.[2] The 12 remaining species are classified into 14 coordinate Sahaptin folk taxa as in Table 1.

**Methods**

The primary data of our research are *identifications* of individual plant specimens (fresh or dried) by knowledgeable native speakers of Sahaptin. Secondary data consist of knowledgeable native consultants' responses to ethnographic queries about native concepts phrased as far as possible in native terms (Berlin, Breedlove, and Raven, 1974; Hunn, 1977) and through direct observation of native plant-related activities. During the past 25 years, we have confronted 31 native speakers (representing 9 of the 15 Sahaptin dialects) with 161 specimens representing 26 of the 29 *Lomatium* species known from the Sahaptin home range. Since most specimens were identified by multiple consultants, the total number of identifications supporting the present analysis is 367.

Responses in the primary identification task may range from no recognition of the plant to immediate, confident recognition and naming of the specimen, a *positive naming response* (PNR). Intermediate categories of response range from recognition without knowledge or recollection of the native term, to uncertainty as to recognition or

[2]The unnamed species are: *L. ambiguum* (Nutt.) C. & R., *L. bicolor* (S. Wats.) C. & R., (*L. leptocarpum* C. & R.) (possibly named), *L. brandegei* (C. & R.) Macbr., *L. cuspidatum* M. & C., *L. donnellii* C. & R., *L. geyeri* (S. Wats.) C. & R., *L. hendersonii* C. & R., *L. laevigatum* (Nutt.) C. & R. *L. martindalei* C. & R., *L. nevadense* (S. Wats.) C. & R., *L. quintuplex* Schlessman & Constance, *L. salmoniflorum* (C. & R.) M. & C., *L. simplex* (Nutt.) Macbr., *L. suksdorfii* (S. Wats.) C. & R., *L. tuberosum* Hoover, *L. vaginatum* C. & R., *L. watsonii* C. & R.

TABLE 1. *Lomatium* species clearly named by Sahaptin speakers. Indian language orthography follows Rigsby (in press).[1] Distribution of native terms coded as follows: NW, Northwest dialect cluster; CR, Columbia River dialect cluster; NE, Northeast dialect cluster; jd, John Day dialect; te, Tenino dialect; ty, Tygh dialect; um, Umatilla dialect; yk, Yakima dialect. Uses and habitats cited are the most typical only. Information on uses by Salish and Nez Perce Indians is from Marshall (1977), Turner (1973), and Turner, Bouchard, and Kennedy (1980). Plant nomenclature follows Hitchcock *et al.* (1961).

| Scientific name | (PNRR*) | Sahaptin name/s | Uses | Distribution |
|---|---|---|---|---|
| *L. canbyi* C. & R. | (38/39) | *sikáywa, sikáwiya* (NW)<br>*lúkš* (CR)<br>*lamúš* (NE) | Staple, tuber eaten, boiled or dried whole or as "finger cakes." | Lithosols, n. w. Nev. n. to Douglas Co., Wash., where overlaps Type B. |
| Type A | | | | |
| Type B | | *škúlkul* (NW, CR, NE) | Staple, tuber eaten, baked underground. | Lithosols, Douglas to Spokane Cos., Wash. |
| *L. columbianum* M. & C. | (0/17*) | *axúla* (yk) | Plant avoided. | Talus slopes, locally, Yakima Co., Wash., to Hood River Co., Oreg. |
| *L. cous* (S. Wats.) C. & R. | (16/16) | *x̣áwš* (NW, CR, NE) | Staple, tuber eaten, boiled or dried whole or as "finger cakes." | Lithosols, Whitman Co., Wash., s. and w. through Blue Mtns. to e. base Oregon Cascades. |
| *L. dissectum* (Nutt.) M. & C. | (12/15) | *čalúkš* (NW, CR, NE) | Medicine for people and horses, fish stupefactant, hide tanning agent, shoots and young roots eaten by Salish and Nez Perce Indians. | Talus slopes, throughout. |
| *L. farinosum* (Geyer ex Hook.) C. & R. | | *nikaptát* (NE) | Tubers eaten. | Lithosols, c. Columbia basin of Wash. e. |
| var. *farinosum* | (0/0*) | | | |
| var. *hambleniae* (M. & C.) Schlessman | (2/14) | *maxšlí, maxšní* (NE) | Tubers eaten. | Lithosols, w. of var. *farinosum* to e. base Wash. Cascades s. to Yakima Co., local, Wasco Co., Oreg. |
| *L. gormanii* (Howell) C. & R. | (4/13) | *sasamít'a, sasamít'aya, ťaťamít'a* (NW, CR, NE) | Tubers eaten (NW) or avoided (CR). | Lithosols, e. c. Wash. w. rarely to e. slope Cascade Mtns., rare, n. Oreg. |
| *L. grayi* C. & R. | (16/21) | *xásya* (NW)<br>*latítlatit* (CR)<br>*atuná* (NE) | Sprouts are the first "Indian celery" available in late winter, root eaten formerly. | Talus slopes, throughout. |
| *L. macrocarpum* (H. & A.) C. & R. | (26/33) | *púťa* (NW, CR, NE) | Tuber eaten formerly. | Lithosols and slopes, throughout. |
| *L. minus* (Rose) M. & C. | (4/6) | *nak'unk* (jd, um) | Tuber eaten formerly, boiled. | Basalt drainage channels, n. c. Oreg. |
| *L. nudicaule* (Pursh) C. & R. | (28/30) | *x̣amsí* (NW, CR, NE) | Peduncles and leaf shoots eaten fresh, seeds used as insect repellent, perfume, and medicine. | Dry open areas, throughout. |
| *L. piperi* C. & R. | (28/31) | *mámin, mámils* (NW, CR, NE) | Favorite, tuber eaten, mixed with *cous* or *canbyi* to make "finger cakes." | Lithosols, e. slope Cascade Mtns. |
| *L. triternatum* (Pursh) C. & R. | (4/30) | *ťáqimaš* (te, ty) | Formerly used as food and medicine, ignored by other Sahaptin speakers. | Dry open areas, throughout. |

*PNRR = Positive Naming Response Ratio. This is the ratio of instances of confident recognition and naming of individual specimens by individual informants to all instances in which an informant was shown a specimen of *Lomatium*. In cases citing no positive naming responses, the referential range of the Sahaptin term is inferred from secondary data.

naming, to misidentifications. One hundred seventy-nine positive naming responses here establish the correspondence of Sahaptin categories to scientific species or subsets of species of the genus *Lomatium*. Two additional Sahaptin categories are defined on the basis of verbal descriptions and secondary data. We indicate in Table 1 ratios of positive naming responses to total identifications (PNR ratios) as an index of the confidence and generality of our Sahaptin-Latin nomenclatural equations.

Secondary data include notes on each species' use as food or medicine, when and where each was harvested, and how each was prepared for consumption or storage. We have recorded native language descriptions of morphological characteristics of plants relevant to their classification and recognition. In addition, we have personally observed contemporary root digging activities, food preparation techniques, and ceremonial feasts.

Hunn has initiated an investigation of the patterns of abundance of each species within the Sahaptin range and of likely rates of harvest under traditional technological constraints. This study has involved transect censuses of populations of several staple species at traditional digging sites to estimate maximal levels of abundance. Densities were sampled along a 50 x 0.2 m transect counted at 1 m intervals. Each transect is thus a sample of fifty 0.2 sq m rectangles oriented randomly with respect to patterns of plant dispersion. All plants were counted regardless of size. Harvest rates were measured by counting the roots dug by an expert Indian woman in five minute intervals at a normal working pace. These calculated rates may be extrapolated on the basis of eight hours work per day and then compared with ethnographic estimates of daily harvest yields. These two independent estimates of daily harvest are in close agreement on an average figure of approximately 30 kg/day (Hunn, 1981).

**Discussion and Results**

The cultural significance of the lomatiums is clearly expressed in the native terminological distinctions. All the common, widespread species, as well as two of restricted range, are well known and differentiated at or below the scientific species level. This expression is remarkable in that the genus is considered "notoriously difficult" by botanical systematists (Hitchcock *et al.*, 1961). Ten *Lomatium* species of the folk system precisely correspond to scientific species. Two scientific species are "split" by the native taxonomists, and two other species, "lumped" by the authoritative regional flora (Hitchcock *et al.*, 1961), are differentiated in the Sahaptin system. These differences do not indicate a fundamental divergence between folk and scientific approaches to classification of natural discontinuities (cf. Berlin, Breedlove, and Raven, 1966); rather, they prove the basic equivalence of those approaches to recognition of species. *Lomatium farinosum* (Geyer ex Hook.) C. & R. is split in the folk system, but precisely along the lines of varietal difference recognized in the most recent scientific treatment (Schlessman, 1978). The differentiation of *L. gormanii* (Howell) C. & R. and *L. piperi* C. &. R. by Sahaptin speakers accords with one scientific opinion in an ongoing taxonomic debate (Mathias, 1938). Although the differentiation of *L. farinosum* var. *farinosum* from var. *hambleniae* (M. & C.) Schlessman is based on flower color, an obvious and relatively superficial distinction, the differentiation of *L. gormanii* from *L. piperi* is based on multiple aspects of morphology, habitat preference, and taste. Similar multiple criteria are involved in the final instance of folk hyper-differentiation of *Lomatium* species, the Northeast Sahaptin distinction between *lamúš* and *škúlkul*, two forms of *L. canbyi* C.

& R., which is unique in that no formal scientific correlate for the distinction is yet known. Clearly, Sahaptin speakers are intensely interested in the lomatiums and are careful observers of *Lomatium* morphology and natural history.

Hewes, in an influential analysis of the native resource base in the Pacific salmon area, claims that the "satisfaction of food energy demand must have been largely up to the fisheries. . . , since *other natural foods available in the area in quantity are notoriously low in fuel value*," (emphasis added) (Hewes, 1973). This key assumption may be more nearly correct for the coastal portion of the Pacific salmon area (Suttles, 1968), but it is clearly false for the interior. The role of the tuberous *Lomatium* species, especially of the staples, *L. canbyi* and *L. cous* (S. Wats.) C. & R., as a source of food energy is clear. *L. canbyi* tubers average about 11.0 g (N = 52) and have been found at densities up to 33 plants/sq m. A kilogram of fresh *L. canbyi* tubers provides 1080 KCal (Benson *et al.*, 1973). *L. cous* tubers average 10.5 g (N = 100), were found at densities up to 32/sq m, and provide 1270 KCal/kg fresh. Thus, both *L. canbyi* and *L. cous* could yield about 4,000,000 KCal/ha at peak densities and at 100 percent utilization.

The native foraging strategy involves selecting plants with well developed "tops," since the plants are perennial and the tubers enlarge progressively with age. Digging is also restricted by preference to zones of high density. Such selective practices suggest a conservative harvest rate in the neighborhood of 10 percent. At that rate, 263 sq km of productive habitat or 0.35 percent of the Sahaptin range could have provided the annual caloric requirement of the entire estimated pre-contact Sahaptin population. Since lithosols characterize a "considerable area" within the region (Daubenmire, 1970), the availability of food energy from native plants was not likely a limiting factor.

More likely limiting was the availability of labor. At an estimated harvest rate for roots of near 4 kg/hr, a woman could harvest a year's supply of *Lomatium* tubers for herself and her family (assuming one root digger per family of four) in 400 hours, or ten 40 hour weeks, a period approximately that of the early April to late June period during which most roots are available, with time out for the spring Chinook salmon harvest. Such a schedule might have left just enough time for cleaning, drying, and cooking these and other foods, and for movements between digging sites.

Additional plant food resources provided options, while others extended the harvest season. Bitterroot, *Lewisia rediviva* Pursh, for example, yields calories at a rate nearly equal to the staple lomatiums, i.e., 3.8 kg/hr at 900 KCal/kg. (Benson *et al.*, 1973); but was harvested at the same times and places as the lomatiums. Camas, *Camassia quamash* (Pursh) Greene, the most important plant of the Liliaceae in the region, was harvested most often in early summer or fall. Camas was highly localized in its distribution. However, rich camas meadows were exploited in common by people from a wide surrounding area. The caloric value of camas is comparable to that of *Lomatium* tubers and bitterroot (Konlande and Robson, 1972). Fruits were available after the root harvest season, but their caloric yields were considerably less than for roots (Watt and Merrill, 1963). For example, we estimate that huckleberries, *Vaccinium membranaceum* Dougl. ex Hook., yield less than 1000 KCal/hr compared to about 4700 KCal/hr for *L. canbyi* and *L. cous*.

The significance of *Lomatium* species for the Sahaptin cultures was not limited to calories. *L. grayi* C. & R. and *L. nudicaule* (Pursh) C. & R. were eaten fresh in late win-

ter and early spring by Sahaptin speakers, as were *L. salmoniflorum* (C. & R.) H. & C. and *L. dissectum* (Nutt.) M. & C. in adjacent areas of the Columbia basin (Marshall, 1977; Palmer, 1975b; Turner, 1973; Turner, Bouchard, and Kennedy, 1980). Nutritional analysis has shown the young stems of *L. nudicaule* to contain 66 mg of ascorbic acid per 100 gm portion (56 cut stems = 100 gms) (Benson *et al.*, 1973). Though the other species cited have not yet been analyzed for this vitamin, their young vegetative growth is quite likely also a rich source.

#### Conclusion

Ethnobotanical data provided by contemporary Sahaptin speakers and summarized here clearly indicate that the genus *Lomatium*—largely unnoted in the published ethnography of the Columbia Plateau—was a primary resource for native subsistence here, as both a staple providing food energy to balance the rich protein yield of the native salmon fishery and as a source of at least one essential vitamin at a critical stage of the seasonal cycle. This resource, processed by women, has strong cultural recognition, based on the Sahaptins' past and ongoing empirical observations.

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# Factors Contributing to the Maintenance of Oligotrophy in an Alpine Glacial Moraine Lake (Wallowa Lake) in Northeast Oregon[1]

**Abstract**

The limnology of renowned Wallowa Lake in northeast Oregon has been largely ignored despite (1) the lake's importance as a landmark attraction in the Wallowa Mountains, (2) its past reputation as a famous spawning site for sea-run salmon and (3) concern over the effects of proliferating recreation and land-use activities on lake quality and longevity. This study found that the lake has remained in remarkably good condition, even though it is regularly subjected to intensive use. Factors such as (1) the relatively barren, rugged watershed terrain, (2) the nutrient impoverished nature of watershed soils, (3) high elevation, (4) rigorous climate, (5) steep, deep lake basin morphometry, (6) effective sewage waste disposal, (7) lake flushing resulting from substantial lake drawdown in summer, and (8) replenishment of lake volume with low temperature and low nutrient inflow water all may contribute to the maintenance of exceptional lake quality and the continuance of Wallowa Lake as a pristine, oligotrophic environment.

## Introduction

Fewer than 10 percent of Oregon's 1650 natural lakes are found in the rugged, remote Blue Mountain Region which lies in the northeast corner of the state (Larson and Donaldson, 1971). Wallowa Lake, located near Joseph, Oregon, in south central Wallowa County (Fig. 1), is by far the largest, most widely known, most accessible and, consequently, most heavily used lake in the region.

Historically, Wallowa Lake was one of few non-coastal lakes of the Pacific Northwest used for spawning by migratory salmonids. Until about 1890, sockeye salmon, *Oncorhynchus nerka*, migrated freely from the Pacific Ocean through the Columbia, Snake, Grande Ronde, and Wallowa rivers, a distance of about 1010 km, to spawn in the lake's inflow tributaries (Fig. 1). In 1890, the lake was impounded by an irrigation dam which severely restricted fish passage. In 1916, a larger dam for power generation was emplaced at the outlet (Fig. 1). This dam terminated anadromous fish runs permanently; as a consequence, some fish, which came to be known as kokanee salmon, remained in the lake as a landlocked population (Bartlett, 1975).

Recreational use of Wallowa Lake has increased dramatically in recent years—from 226,000 visitors in 1955 to over one million lake users in 1966 (Oregon State Board of Health, 1966). Lakeside residences have also increased, from a scattered few in the 1940s to about 300 in 1971. As a result, local governments and citizens expressed serious concern about the possibility of watershed deterioration and lake pollution due to accelerated tourism, commercialism, and real estate development.

Despite its reputation, popularity, and alleged vulnerability, little has been done to

[1]This work was supported by the Water Quality Studies Program, Oregon Department of Environmental Quality, Portland.

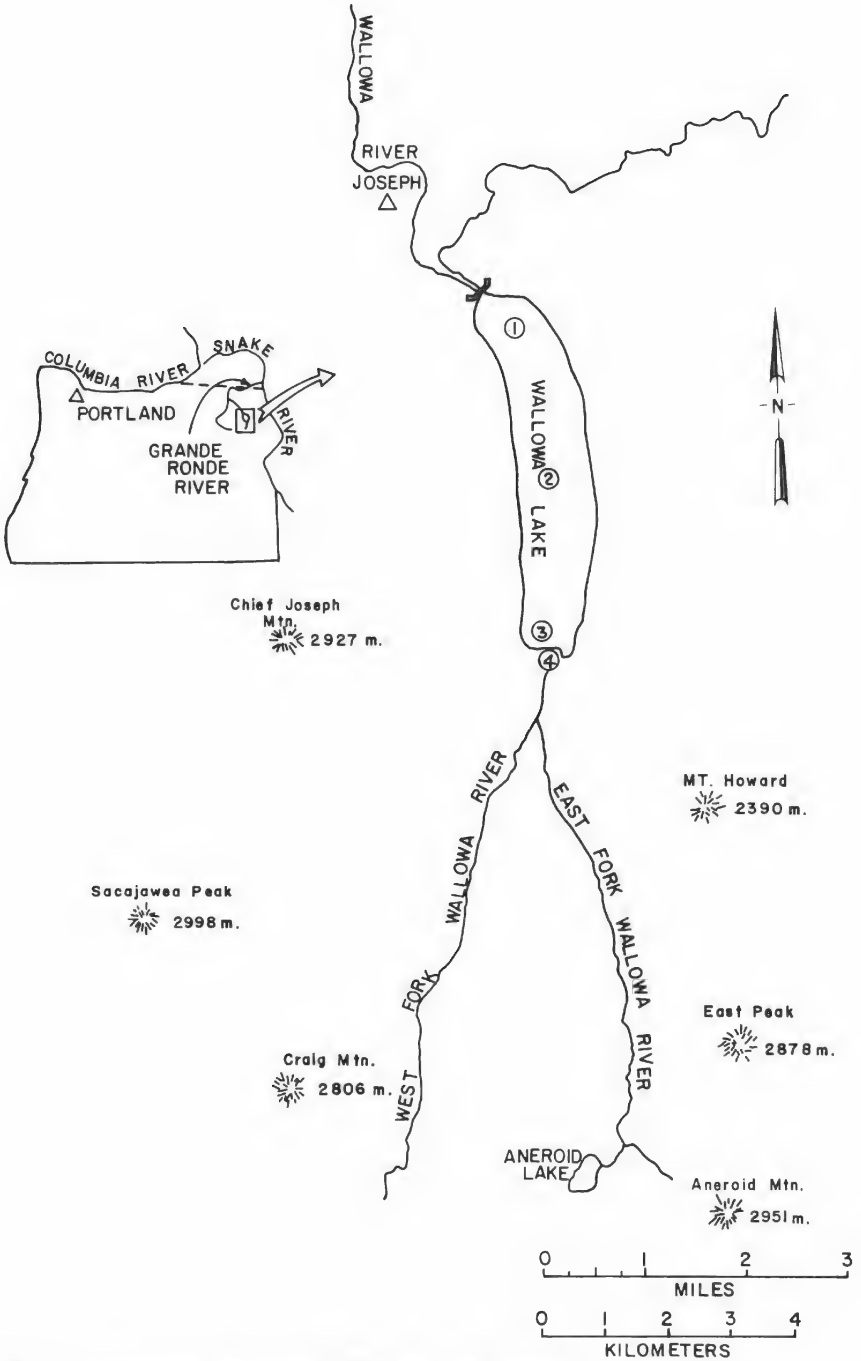


Figure 1. Location and outline map of Wallowa Lake, Oregon.

assess the response of Wallowa Lake to cultural use. In fact, the limnology of the lake is poorly known. This work, completed during the summer of 1973, provides limnological data to serve as a point of reference for future investigators and, through the process of evaluating forces that influence lake quality and eutrophication, addresses the question of lake degradation.

### Earlier Investigation

Wallowa Lake was probably first studied in the 1890s by scientists such as Evermann and Meek (1897) who were interested in the lake as a potential salmon fishery. During 1911-1912, the U.S. Geological Survey in cooperation with the Oregon State Engineer completed a thorough mineral analysis of water collected from the Wallowa River at a point approximately 100 m downstream of the dam outlet at the north end of the lake (Van Winkle, 1914). The geological physiography and the origin of Wallowa Lake were described by Stovall (1929) and Smith and Greenup (1939), respectively.

In a lake survey report by the Oregon Game Commission (Pillow, 1941), Wallowa Lake was regarded as a "problem" lake because of its relatively limited abundance of fish food organisms due primarily to the lake's deep, steep-walled, gravel-bottomed basin filled with relatively high quality water which generally restricted biological productivity, including fish production. The Oregon Game Commission admitted that repeated large plantings of eastern brook trout, *Salvelinus fontinalis,* had failed at Wallowa Lake; the Commission recommended, instead, that the lake be stocked exclusively with fingerling (about 8 cm long) rainbow trout, *Salmo gairdneri,* at a rate of about 60,000 per year. It concluded further that kokanee salmon, then the predominant fish in the lake, were abundant enough to sustain themselves without restocking in spite of heavy fishing pressure. More recently, the Fish Commission of Oregon conducted a kokanee salmon rehabilitation study at Wallowa Lake (Thompson, 1959), and the Oregon Department of Environmental Quality (D.E.Q.) assembled a list of the lake's planktonic organisms (McHugh, 1972). During the period 1966-1972, the Oregon Health Division and D.E.Q conducted yearly water quality and sanitary surveys (O.S.B.H., 1966; McHugh, 1972) at the request of local community organizations.

### Physical Description of Wallowa Lake

#### Geomorphology

Wallowa Lake is located in northeastern Oregon, approximately 40 km west of the Snake River and 72 km south of the Oregon-Washington border (Fig. 1). The combined events of glacial scour and the subsequent damming of the Wallowa River by lateral and terminal moraines (Smith and Allen, 1941) formed a long, narrow lake basin, approximately 6.5 km long and 1.0-1.5 km wide, and situated on a north-south length axis. Surface area is 7.9 $km^2$; surface elevation is 1336 m (above m.s.l.).

Wallowa Lake is fed chiefly by the Wallowa River, which enters from the south (Fig. 1). Because of its steep longitudinal gradient, the river flows turbulently at relatively high velocities which enable it to transport a substantial load of coarse sediments. These are deposited rapidly at the south end of the lake where the river emerges, forming a prominent alluvial delta which continues to build lakeward and fill the basin. As the river crosses the delta on its way to the lake, rapid deposition of coarse materials

due to decreased stream gradient and velocity forces the main stream channel to ramify and shift laterally, producing a braided stream pattern.

The Wallowa River continues to flow northward through an outlet at the north end of the lake. There, the dam installed years earlier regulates lake surface elevation and downstream releases, and supplies water for irrigation and domestic uses.

Lake volume has varied considerably in past years, ranging from 58,998 x $10^3$ $m^3$ in June 1957 to 5908 x $10^3$ $m^3$ in October 1929 (U.S.G.S., 1978). Regulated discharge from the lake averaged 3.8 $m^3sec^{-1}$ in a 50-year period (1928-1977), with the maximum release flow (43.9 $m^3sec^{-1}$) occurring in June 1969 (U.S.G.S., 1978). Zero discharge has occurred periodically during particularly dry years (U.S.G.S., 1978).

### Climate

The climate of the Wallowa Lake region is rigorous, particularly during winter months. Annual mean temperature and annual mean precipitation for a ten-year period (1951-1960) were 6.1°C and 34.8 cm, respectively (U.S. Weather Bureau data compiled at Enterprise, located about 10 km northwest of the lake, 1965). Winter temperatures have been known to reach –38°C, whereas daytime summer temperatures easily exceed 39° C (U.S.W.B., 1965). Generally, precipitation as snowfall occurs from October through April, with trace amounts having been recorded in July (U.S.W.B., 1965). Mean annual snowfall, recorded at Wallowa, Oregon (located about 40 km northwest of the lake), was 106.7 cm for the period 1951-1960 (U.S.W.B., 1965).

### Basin Morphometry and Bottom Composition

The lake basin is of glacial origin, featuring a deep, elongate, steep-walled trough, bounded on both sides by high, angular lateral moraines that rise nearly 300 m above the surface of the lake (Smith and Allen, 1941).

Maximum lake depth is about 92 m; shoal area (0-5 m depth) is practically nonexistent (Pillow, 1941). The lake bottom is paved largely with sand, gravels, and boulders (Smith and Allen, 1941).

## Methods

Limnological surveys were conducted at Wallowa Lake during June and August 1973. Water samples for chemical and biological analyses were collected near the lake surface (1-2 m depth) at three sites and from the Wallowa River before it entered the lake (Fig. 1). At the midlake station (Station 2), water samples were also collected near lake bottom with a 2.5*l* Van Dorn PVC water bottle.

Vertical temperature profiles were recorded at Station 2 using a Yellowsprings telethermometer (model 43TD, scale calibrated in 1.0°C units). Determinations for dissolved oxygen were by Winkler technique (azide modification) (APHA, 1971). Water transparency was measured with a 20 cm Secchi disc. Procedures for determining other water quality parameters are given as follows.

*Conductivity, Specific*: Temperature compensated bridge in laboratory; unpreserved.

*Alkalinity*: Titration with 0.02N $H_2SO_4$ using pH end-points of 5.1 for alkalinity $<100$, 4.8 100-300, 4.5 $>300$; unpreserved. 13th ed. *Standard Methods*. 102, pg. 52.

*Color*: Comparator with permanent glass standards; unpreserved.

*Turbidity*: Hach turbidimeter; formazin standard; unpreserved.

*Suspended Solids* (non-filtrable residue): pre-washed and tared Millipore filters (47 mm 0.8 $\mu$m pore size); unpreserved.

*Soluble Orthophosphate*: Filtrate from suspended solids determination; molybdophosphoric—stannous chloride reduction; preserved by refrigeration. 13th ed. *Standard Methods.* 223C II, pg. 525.

*Total Phosphate*: Sulfuric acid-nitric acid digestion; stannous chloride method; preserved by refrigeration. 13th ed. *Standard Methods.* 156C, pg. 334.

*Sulfate*: Turbidimetric with $BaCl_2$; unpreserved. 13th ed. *Standard Methods.* 156C, pg. 334.

*Chloride*: Titrimetric with $Hg(NO_3)_2$; unpreserved.

*Total Dissolved Solids* (filtrable residue): Tared porcelain dishes; steam bath evaporation of filtrate; residue dried to constant weight in an oven at 105°C; analytical balance; filtered sample; unpreserved. 13th ed. *Standard Methods.* 148B, pg. 290.

*Hardness*: EDTA titration; unpreserved. 13th ed. *Standard Methods.* 122B, pg. 179.

*Na*: Flame photometry; acid preserved.

*K*: Flame photometry; acid preserved.

*$NH_4$-N*: Colorimetric bertholot (phenate) reaction; $HgCl_2$ preserved. 13th ed. *Standard Methods.* 132C, pg. 232.

*$NO_3$-N*: Brucine method; $HgCl_2$ preserved. 13th ed. *Standard Methods.* 213C, pg. 461.

*$NO_2$-N*: Colorimetric azo dye; $HgCl_2$ preserved. 13th ed. *Standard Methods.* 134, pg. 240.

*Kjeldahl-Nitrogen*: Automated technicon method; digestion followed by $NH_4$-determination, $HgCl_2$ preserved.

Water (48*l*-volume) for phytoplankton analyses was filtered through a Kahl nannoplankton net (mesh aperture diam. = 28 $\mu$m). Material collected was preserved with 5 percent formalin and examined microscopically under oil immersion (1000X magnification). Individual cells or colonies were identified, but not enumerated for quantitative purposes.

Biochemical oxygen demand (5-day incubation) and coliform bacteria (multiple tube technique) were determined in accordance with *Standard Methods* (A.P.H.A., 1971).

## Results

### Thermal characteristics

Wallowa Lake is classified as a dimictic lake because of two yearly mixing periods or turnovers which occur in spring and fall. During a typical winter, the lake surface is covered with a layer of ice ranging in thickness from a few centimeters to as much as 0.5 m (R. McHugh, pers. comm.). In summer, the lake stratifies thermally, with the thermocline occurring at about 7 m in early June and 12 m by mid-August (Table 1). Possibly, inflowing Wallowa River water—measuring 6.9°C on 6 June and 11.0°C on 20 August 1973—contributes to the maintenance of a relatively cool summertime epilimnion (Table 1) and an unstable thermocline (Hutchinson, 1957).

### Optical Properties and Suspended Matter

Wallowa Lake exhibits relatively clear water, a feature typical of oligotrophic lakes. Secchi disc transparencies at the midlake station on 6 June and 20 August were 8.5 and

TABLE 1. Vertical temperature gradients for Wallowa Lake, Oregon. Readings in degrees Celsius. 1941 profile by Pillow (1941).

| Depth (m) | 9/6/41 | 6/6/73 | 8/20/73 |
|---|---|---|---|
| Surface | 15.6 | 14.5 | 17.7 |
| 2 | | 13.3 | 17.6 |
| 3 | 14.4 | | 17.5 |
| 4 | | 12.0 | 17.3 |
| 6 | 15.0 | 11.1 | 17.0 |
| 8 | | 10.3 | 16.3 |
| 9 | 15.0 | | |
| 10 | | 9.9 | 14.7 |
| 12 | | 8.1 | 10.8 |
| 14 | | 7.0 | 9.4 |
| 15 | 12.2 | | |
| 16 | | 6.2 | 8.0 |
| 18 | 10.0 | 5.5 | 6.6 |
| 20 | | 5.1 | 5.3 |
| 22 | | 4.9 | |
| 23 | 6.7 | | |
| 24 | | 4.8 | |
| 25 | | | 5.0 |
| 30 | | 4.5 | 4.1 |
| 31 | 6.1 | | |
| 38 | 5.0 | | |
| 46 | 5.0 | | |
| 55 | | | 3.9 |
| 61 | 5.0 | | |
| 65 | | | 3.8 |
| 78 | | 4.4 | |

TABLE 2. Secchi disc transparencies compared between Wallowa Lake and other "oligotrophic" lakes in Oregon.

| | Secchi depth (m) |
|---|---|
| Wallowa Lake (6/6/73) | 8.5 |
| Wallowa Lake (8/20/73) | 13.7 |
| Crater Lake (8/5/69) (Larson, 1972a) | 39.0 |
| Odell Lake (8/13/68) (Larson, 1972b) | 7.9 |
| Woahink Lake (8/6/68) (Larson, 1972b) | 6.4 |
| East Lake (7/11/68) (Larson, unpub.) | 7.6 |
| Paulina Lake (7/10/68) (Larson, unpub.) | 7.9 |
| Waldo Lake (8/6/69) (Larson, 1978) | 27.0 |
| Cultus Lake (8/15/68) (Larson, unpub.) | 18.6 |
| Collard Lake (8/21/72) (Larson, 1974) | 5.5 |
| Mercer Lake (8/5/68) (Larson, 1974) | 4.6 |

13.7 m, respectively, which compare fairly well with other "oligotrophic" lakes in Oregon (Table 2).

High transparency or clarity of lakewater, as opposed to high turbidity, is generally attributed to (1) low production of organic materials within the lake, (2) high settling velocity of incoming soil materials such as sand, and (3) sediment deposition in deep, relatively undisturbed waters. These conditions account for its moderately high Secchi disc transparencies. Turbidity (Table 3) increases with an increase in the concentration of suspended organic and inorganic solids that are generated autochthonously or derived from the surrounding watershed (allochthonous). In either case, the result is a decrease in transparency. For Wallowa Lake, most of the incoming soil materials derived from the watershed and the shoreline are coarse in texture, which allows them to settle

TABLE 3. Water quality, Wallowa Lake and Wallowa River, Oregon, 1973.

| Parameter | 6 June Stations | | | | 20 August Stations | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Turbidity, J.T.U. | <1 | <1(<1)[1] | <1 | 1.0 | 1.0 | <1(<1)[1] | 1.0 | <1 |
| Total residue, mg/l | 64 | 68(76) | 65 | 49 | 96 | 91(107) | 76 | 76 |
| Non-Filtrable residue, mg/l | 0.5 | <0.5(<0.5) | <0.5 | 1.0 | <0.5 | <0.5(<0.5) | <0.5 | <0.5 |
| Color | <1 | <1(<1) | <1 | <1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Sodium, mg/l | 2.0 | 1.0(2.0) | 2.0 | 0.5 | 3.2 | 1.5(1.8) | 1.5 | 1.8 |
| Potassium, mg/l | 0.5 | <0.5(0.5) | 1.0 | 0.5 | 0.9 | 0.7(0.9) | 0.7 | 0.9 |
| Chloride, mg/l | 1.6 | 1.1(1.1) | 1.1 | 1.1 | 0.9 | 0.4(0.4) | 0.4 | 0.4 |
| Sulfate, mg/l | 5.5 | 5.5(6.5) | 6.0 | 2.8 | 7.5 | 4.6(6.0) | 5.3 | 4.7 |
| Total alkalinity, mg/l as $CaCO_3$ | 42.0 | 42.0(47.0) | 44.0 | 23.0 | 40.0 | 38.0(46.0) | 40.0 | 41.0 |
| Total hardness, mg/l as $CaCO_3$ | 44.4 | 45.2(49.2) | 46.0 | 23.2 | 42.3 | 38.8(46.7) | 40.7 | 39.0 |
| Conductivity, micromhos/cm | 103 | 120(130) | 122 | 71 | 114 | 113(132) | 112 | 118 |
| pH | 7.6 | 7.8(7.4) | 7.6 | 7.5 | 7.8 | 7.8(7.5) | 7.8 | 7.7 |
| Ammonium-nitrogen, mg/l | 0.07 | 0.03(0.04) | 0.04 | 0.01 | 0.12 | 0.04(0.02) | 0.01 | <0.01 |
| Nitrate-nitrogen, mg/l | 0.12 | 0.09(0.12) | 0.08 | 0.09 | <0.01 | <0.01(<0.01) | <0.01 | 0.03 |
| Kjeldahl nitrogen, mg/l | 0.1 | <0.1(<0.1) | <0.1 | <0.1 | 0.3 | 0.2(0.2) | 0.2 | 0.2 |
| Orthophosphate, mg/l | 0.01 | 0.01(0.02) | 0.01 | <0.01 | 0.25 | 0.07(0.06) | 0.05 | 0.07 |
| Total phosphorus, mg/l | <0.1 | <0.1(<0.1) | <0.1 | <0.01 | 0.7 | <0.1(<0.1) | <0.1 | <0.1 |
| Dissolved oxygen, mg/l | 10.0 | 10.0(9.6) | 9.6 | 10.1 | 8.4 | 8.4(8.7) | 8.4 | 9.3 |

[1]Values in parentheses represent data for near-bottom lake sample.

quite rapidly. Usually, less than one percent of the total solid content in Wallowa Lake is suspended (i.e., non-filtrable residue) (Table 3). An overwhelming percentage of the total solids is dissolved.

Wallowa Lake water is essentially colorless. Color units, expressing the degree of lakewater coloration usually due to the presence of dissolved organic and inorganic substances, were generally less than one and occasionally zero (Table 3).

### Chemical Features

The water chemistry of Wallowa Lake approximates that of several other "oligotrophic," dilute-water lakes located farther west in the Oregon Cascade Range. Surprisingly, in some cases, Wallowa lakewater is less enriched chemically than the water of famously pristine Crater Lake, Oregon (Table 4). Moreover, lakewater quality appears to have changed very little between the years 1911 and 1973 (Table 5).

Generally, concentrations of major ions are relatively low (Table 3). Sodium, potassium, chloride, and sulfate together constitute only about 5 percent of the total dissolved solid content which, in 1973, averaged 76.8 mg/*l*. Van Winkle (1914) reported that 98.4 percent (average) of the total ion composition consisted of calcium and bicar-

TABLE 4. Water chemistry: Wallowa vs. Crater Lake, Oregon.

| | Crater Lake[1] | Wallowa Lake[2] | |
|---|---|---|---|
| | | 6 June | 20 August |
| Sodium, mg/l | 7.5 | 1.0- 2.0 | 1.5- 3.2 |
| Potassium, mg/l | 1.8 | <0.5- 1.0 | 0.7- 0.9 |
| Chloride, mg/l | 7.4 | 1.1- 1.6 | 0.4- 0.9 |
| Sulfate/mg/l | 15.3 | 5.5- 6.5 | 4.6- 7.5 |
| Total dissolved solids, mg/l | 81 | 64 - 76 | 91 -107 |
| Total alkalinity, mg/l as $CaCO_3$ | 29.1 | 42 - 47 | 38 - 46 |
| Total hardness, mg/l as $CaCO_3$ | 28.9 | 44 - 49 | 39 - 47 |
| Specific conductivity, micromhos/cm | 117 | 103 -130 | 112 -132 |

[1]Phillips and Van Denburgh, 1968; Larson, 1972a.
[2]1973 study, range of values for the three lake stations.

TABLE 5. Mineral analyses of water from Wallowa River near Joseph, Oregon, 18 August 1911-15 August 1912 (Van Winkle, 1914). Samples collected at a point located about 100 m below the dam outlet at the north end of Wallowa Lake. Mean values (n=13), expressed in milligrams per liter, are compared with mean DEQ values (n=7) obtained at Station 1 located near dam outlet. Possible significant differences in chemical methodologies may, however, invalidate data comparisons.

| | 1911-1912 (Van Winkle, 1914) | 1966-1973 (DEQ) |
|---|---|---|
| Turbidity, J.T.U. | 1.0 | 0.9 |
| Suspended Solids, mg/l | 0.9 | 1.5 |
| Color | 1.0 | 0.4 |
| Sodium, mg/l | 4.5 | 2.6 |
| Sulfate, mg/l | 8.5 | 6.6 |
| Chloride, mg/l | 0.6 | 1.4 |
| Nitrate, mg/l | 0.21 | 0.097 |
| Iron, mg/l | 0.02 | — |
| Calcium, mg/l | 15.0 | — |
| Magnesium, mg/l | 0.6 | — |
| Bicarbonate, mg/l | 47 | — |
| Carbonate, mg/l | 0.0 | — |
| Total Dissolved Solids, mg/l | 64 | 59 (Approx.) |

bonate. The relatively low mineralization of Wallowa lake and riverwaters is indicated further by comparatively low values for total alkalinity, total hardness, and specific conductance, and by pH readings that never exceeded 8.0 (Table 3).

Variation in water chemistry among stations was generally small except for the 6 June sampling when Wallowa riverwater (Station 4) was considerably less mineralized than lakewater—presumably because of early summer snowmelt runoff. River alkalinities, hardness, conductivities, and concentrations of sodium and sulfate then were about one-half the lakewater values. By August, however, lower flows had produced more concentrated conditions in the river (Table 3). At the mid-lake station, water collected from near bottom differed chemically from surface water, with deep hypolimnetic alkalinities, hardness, and conductivities being roughly 10-15 percent greater, possibly caused by settling of organic detritus into the hypolimnion where it eventually decomposed and mineralized.

Concentrations of nitrogen and phosphorus—both major basic nutrients for algal growth and productivity—were relatively low (Table 3). The supply of algal nutrients in Wallowa Lake is perhaps not sufficiently large to support excessive nuisance growths of algae typical of more enriched, eutrophic lakes. But populations of lake algae may not respond predictably to such varying levels of nitrogen and phosphorus often expressed as "high," "low," or "critical," although some investigators (Sawyer, 1952) have established finite limits of nutrient concentrations above which blooms of algae might be expected. So-called "high" concentrations of N and P will not necessarily result in overgrowths of algae. Other lake factors may be limiting. On the other hand, relatively small concentrations of N and P may be sufficiently large to produce noticeable algal growths, provided other factors such as illumination, temperature, and the availability of minor nutrients are favorable. Thus, in Wallowa Lake, even though nutrient levels appear to be generally low—at least during the sampling periods—other factors may be of greater importance in determining the lake's relatively low potential for biological production which yields comparatively small crops of algae as well as other aquatic organisms.

Concentrations of nitrogen and phosphorus, similar to those of sodium, chloride and sulfate, were generally highest near the outlet at the north end of the lake (Station 1) (Table 3). Such concentrations are possibly explained by the movement and accumulation of suspended organic materials in that direction due to lake current patterns set up by, among other factors, considerable lakewater withdrawal for irrigation and municipal water supply purposes. During summer 1973, lake volume was reduced to about one-third of its initial summer volume, from 22,636 x $10^3$ $m^3$ on 31 May to 7376 x $10^3$ $m^3$ on 31 August (U.S.G.S., 1974).

Nitrate-nitrogen appeared to be more abundant in early summer (Table 3) when ambient temperature and other conditions were probably least favorable for summertime algal productivity. As summer progressed, however, biological activity increased (in response to warmer temperatures), which tended to deplete available nitrate.

Wallowa Lake was oxygenated to the point of being supersaturated with oxygen at all stations (Table 3). Dissolved oxygen was equally abundant near the bottom of the lake due to low temperatures and the paucity of oxidizable, organic matter capable of exerting biochemical oxygen demand (Table 3). Pillow (1941), upon measuring D.O. in Wallowa Lake on 6 September 1941, reported values of 8.2, 10.3 and 8.3 mg/*l* at

depths of 1, 23, and 61 m, respectively. This kind of vertical distribution of D.O.—featuring a convex-shaped, vertical D.O. curve, with maximum values found at middepth or near-bottom—is termed orthograde, and is characteristic of deep, oligotrophic lakes.

### Biological Features

Biological processes in Wallowa Lake are limited. Conditions which normally would encourage high rates of biological production, decomposition, and organic accumulation are generally lacking. The lake basin, being relatively steep-walled and deep, offers little in the way of a true littoral zone (i.e., shallow, nearshore waters), which, in more enriched, eutrophic lakes, may be extensive, and infested with rooted aquatic plants and undesirable fish and invertebrates. The bottom of Wallowa Lake is covered predominantly with barren sands and gravels, in contact with low temperature water (near 4°C in summer), and is overlain by 60-80 m of water which effectively keeps the bottom in darkness by filtering incident solar radiation. In general, the lake's bottom represents a biologically unfavorably benthic habitat. In the limnetic or open-water zone, seemingly small supplies of inorganic nutrients, perhaps in deficient quantities, generally restrict the abundance of phytoplankton. As primary energy-fixing organisms in the aquatic food-chain, phytoplankton ultimately determine the growth, production, and survival of crustaceans, insects, fish, and other consumer organisms. On 29 March 1966, for example, DEQ personnel reported finding a "few" algae in samples collected by pulling a plankton net horizontally through surface waters for 8-10 minutes at the south end of the lake, whereas in two samples collected at the north end, no algae could be found at all. During the 1973 plankton samplings (Table 6), the most abundant phytoplankter present was *Dinobryon divergens*, which accounted for 60 to nearly 100 percent of the total phytoplankton biomass (i.e., that portion of the phytoplankton biomass collected with a 28 $\mu$m mesh net), although its presence in the lake was not immediately apparent. The predominance of *D. divergens*, a species thought to exist mostly when concentrations of phosphate range between 0.001 and 0.005 mg/*l* (Hutchinson, 1967), suggests that the availability of phosphorus in Wallowa Lake is indeed limited. As a result, other species and groups of algae, deprived of essential phosphorus, never reach the densities attained by *D. divergens*.

TABLE 6. Checklist of phytoplankton collected at Wallowa Lake in 1973.

| Depth | 6 June | 20 August |
|---|---|---|
| Surface | **Dinobryon divergens**<br>**Melosira italica**<br>**Mallomonas producta**<br>**Fragilaria erotonensis** | **Dinobryon divergens**<br>**Ceratium hirundinella** |
| Secchi depth | **Dinobryon divergens**<br>**Mallomonas producta** | **Dinobryon divergens**<br>**Ceratium hirundinella**<br>**Fragilaria erotonensis** |

Small numbers of coliform bacteria were found in samples collected from Wallowa Lake and vicinity (Table 7). Only once during the seven DEQ surveys (1966-1973) did MPN values exceed 62 (per 100 milliliters sample volume) at any of the sampling stations. During the 1973 survey, MPN values were usually less than 45. Similarly, the Oregon Health Division (OSHB, 1966) found exceptionally low concentrations of

TABLE 7. Most probable number (MPN) of coliform group organisms per 100 milliliters and biochemical oxygen demand (BOD) for Wallowa Lake and Wallowa River, Oregon, 1966-1973. BOD in milligrams per liter.

| Station | 3/29/66 | | 8/2/66 | | 4/20/70 | | 9/8/70 | | 8/9/71 | | 6/6/73 | | 8/20/73 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MPN | BOD | MPN | BOD | MPN | BOD | MPN | BOD | MPN | BOD | MPN | BOD | MPN | BOD |
| 1 | <4.5 | 0.4 | <45 | 0 | <4.5 | 0.8 | <4.5 | 1.2 | 21 | 0.1 | <45 | 0.3 | <45 | 0.3 |
| 2 | <4.5 | 1.1 | <45 | | <4.5 | 0.6 | <4.5 | 0.9 | 25 | 0.3 | <45[1] | 0.3[2] | <45[1] | 0.6[2] |
| 3 | <4.5 | 0.6 | <45 | 0.3 | <4.5 | 0.7 | <4.5 | 0.9 | 13 | 0.1 | <45 | 0.1 | <45 | 0.2 |
| 4 | <4.5 | 0.5 | 23 | 0.5 | <4.5 | 0.7 | <4.5 | 1.1 | 6 | 0.1 | <45 | 0.3 | <45 | 0.1 |

[1]MPN values for near-bottom lake samples were <45 on both sampling periods in 1973.
[2]BOD values for near-bottom lake samples were 0.3 mg/l on 6 June and 0.1 mg/l on 20 August.

coliform bacteria even in a portion of the lake used as a swimming area (Table 7).

Low biochemical oxygen demands (BOD) reflected the low biotic potential of Wallowa Lake (Table 7). During the 1966-1973 DEQ surveys, BODs averaged only 0.51 mg/*l* (mean of 61 determinations), which was 0.11 mg/*l* lower than the mean BOD (32 determinations) recorded for an exceptionally oligotrophic coastal lake (i.e., Woahink Lake) in 1972 (Larson, 1974).

### Discussion

In view of the foregoing information, Wallowa Lake and the upper reaches of the Wallowa River are relatively clean, unpolluted, uncontaminated waters. In terms of natural beauty and degree of water purity, Wallowa Lake ranks high among other pristine lakes in Oregon. Lake quality, however, may deteriorate slightly in summer if substantial nutrient loading produces noticeable blooms of algae. But no one, to the author's knowledge, has ever reported a dense, sustained, "pea soup" algal bloom on Wallowa Lake, although McHugh (1972) described the abundance of *Dinobryon divergens* in 1970 and 1971 as "blooms." Surface accumulations of pollen, blown into the lake from forested areas in the watershed, have occasionally been mistaken for algal blooms.

The aesthetic and ecological properties of Wallowa Lake will certainly not improve under the influence of ever-increasing recreational uses and real estate subdivisions. Fortunately for Wallowa Lake, the impact of man's presence may be lessened somewhat by circumstances attributed to both man and nature. According to the Oregon Health Division, for example, sewage disposal systems are still few in number, are widely distributed along a lengthy lakeshore frontage, are used almost exclusively in summer, thus affording drainage soils time to recharge and recover for the following year, and are located mostly in fine-particled soils at distances (15 m or greater) from the lake, allowing for adequate filtration and treatment of sewage trickling flows. In addition, the relatively barren regolith that dominates watershed and lake bottom surfaces and the morphometry of the lake basin (being steep-walled, deep and so large in volume that present inputs of sewage and other lake-deteriorating wastes are possibly diluted to the point of being inconsequential) contribute to the lake's comparatively low biotic potential and high water quality. Moreover, the summer release of lakewater through the dam outlet for irrigation purposes, which was substantial in 1973, may remove significant quantities of phytoplankton standing stock, inorganic nutrients and organic detritus which otherwise would concentrate in the lake and presumably result in less desirable aquatic conditions. Inflowing tributary water, principally the Wallowa River

which enters at the south end of the lake and replaces some of the lakewater lost through withdrawals, evaporation, and ground water seepage, may actually diminish rates of biological production and decomposition because of its "newness." Water newly introduced into a lake system may be physiologically and ecologically less favorable to algae and bacteria than water that has been standing in one place for a considerable length of time. Most algae may function poorly until they have had sufficient time to acclimate to "new" water (Findenegg, 1965).

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# Response of Steppe Shrubs to the 1977 Drought[1]

**Abstract**

Litterfall collecting is a non-destructive and efficient way to monitor the leaf growth of steppe shrubs over extended periods of time. During the 1977 growing season, the shrub steppe region experienced severe drought. Shrubs responded by producing few leaves, resulting in less litterfall. In some areas, spiny hopsage did not produce leaves at all. The drought was broken in 1978: sagebrush, bitterbrush, spiny hopsage, and greasewood produced as much or more litterfall as they did in the 1976 growing season.

## Introduction

Although drought is an annual experience for plants growing on the Hanford Site in southcentral Washington, it was especially prolonged during the 1976-77 plant growing season. Herbaceous productivity was reduced in 1977 as compared to previous years and shrubs were also affected. This paper reports monthly collections of shrub litterfall in the years before, during, and after the 1977 drought. Litterfall has been used as a way to estimate productivity of forest communities; however, it has seldom been used to estimate shrub production in semi-arid regions (Mack, 1977). In forest regions, the trees are of economic concern because of the value of wood. In shrub-steppe regions, grasses are usually the subjects of concern because shrubs (e.g., sagebrush) are poor livestock forage as compared to grasses (Daubenmire, 1970). This study presents a way to monitor temporal and spatial differences in chemical composition of shrub leaves in a non-destructive fashion through litterfall collections. The data also indicate that leaf fall collecting is an efficient way to obtain information concerning the impact of drought upon the leaf growth of steppe shrubs.

## Methods

Collectors made of short lengths of plastic irrigation pipe (polyvinyl chloride, PVC) were used to collect litterfall from individual shrubs. Each collector consisted of a one decimeter length of 15.6 cm diameter pipe and a 0.5 dm length of the same pipe. The two pieces were cemented together after putting in place a piece of nylon mesh screen to serve as a floor to the collector. The mesh permitted rainfall to pass through the collector, but leaves and other plant parts were retained. One collector was placed under the canopy spread of each shrub with the tall section above the short section. Each collector was emptied of its accumulated contents at the beginning of each month. These devices were heavy enough to remain in place under the most windy conditions

[1]This study was prepared for the U.S. Department of Energy under Contract No. DE-AC06-RLO 1830.

and also deep enough to keep leaves from blowing away once they were in the collector. The collected plant material was hand-sorted in the laboratory to exclude any large twigs or animal debris; the remainder was air dried before weighing.

Four species of shrubs were selected for study, greasewood (*Sarcobatus vermiculatus*), spiny hopsage (*Atriplex spinosa*), butterbrush (*Purshia tridentata*), and sagebrush (*Artemisia tridentata*). At each site, four individual shrubs of each species were provided with collectors. The shrubs were all located on the Arid Lands Ecology Reserve at the locations shown below.

| Taxa | Location | Elevation (ft.) |
|---|---|---|
| Hopsage and greasewood | Rattlesnake Spring | 690 |
| Bitterbrush | Southeast ALE | 440 |
| Sagebrush | ALE Headquarters | 1080 |
| Sagebrush | Rattlesnake Mountain | 3130 |

Rain gauges were maintained at three of these sites and were read monthly.

**Results and Discussion**

The results of litterfall collections are summarized in Figure 1. Hopsage averaged 2.12 g of dry litter during the first season, 1976. No measurable litter was collected in 1977 because hopsage failed to produce a crop of leaves that year. However, in 1978 hopsage averaged 3.65 g of litter per collecting device. The 1978 litterfall collections were marked by an abundance of winged fruits. July was the month of peak litterfall collection in 1976 and 1978.

Bitterbrush produced on the average 2.95 g of litter in 1976, 0.77 g in 1977, and 3.70 g in 1978. August was the peak month of litterfall collection. The duration of litterfall in 1978 extended later into the autumn than it did in 1976 and 1977 (Fig. 1).

Greasewood produced more litterfall than other shrub species, partly because of larger plants. Litterfall averaged 5.33 g in 1976 and only 1.29 g in 1977. Clearly, greasewood litterfall was influenced by the 1977 drought even though greasewood has deep root systems and is regarded as a phreatophyte (Harr and Price, 1972). The peak month of litterfall in 1976 was November (Fig. 1). In 1978 litterfall averaged 8.87 g; unlike the previous years, the peak month of litterfall was September (Fig. 1).

Sagebrush is by far the most abundant shrub species on the Arid Lands Ecology Reserve; two sites were studied, a low elevation site and a high elevation site (Fig. 1). The low elevation site in 1976 yielded 2.69 g of litterfall but only 1.46 g in 1977. As were the other shrub species, sagebrush was affected by the 1977 drought. In 1978 sagebrush recovered from the drought and produced 3.99 g of litterfall. There was no definitive peak month of litterfall in 1977, but July was the peak month for litterfall in 1978 (Fig. 1).

Sagebrush at the high elevation site produced 2.14 g of litter in 1976 and 2.88 g in 1977. The effect of drought on sagebrush at the higher elevation was not so apparent. In 1978 litterfall amounted to 5.09 g. July was the peak month of litterfall during all three years, but August 1978 was also a heavy producer (Fig. 1).

The monthly precipitation measured at three of the study sites is summarized in Figure 2. As expected, precipitation was greatest at the high elevation. The October to May precipitation corresponds to the most active portion of the plant growing sea-

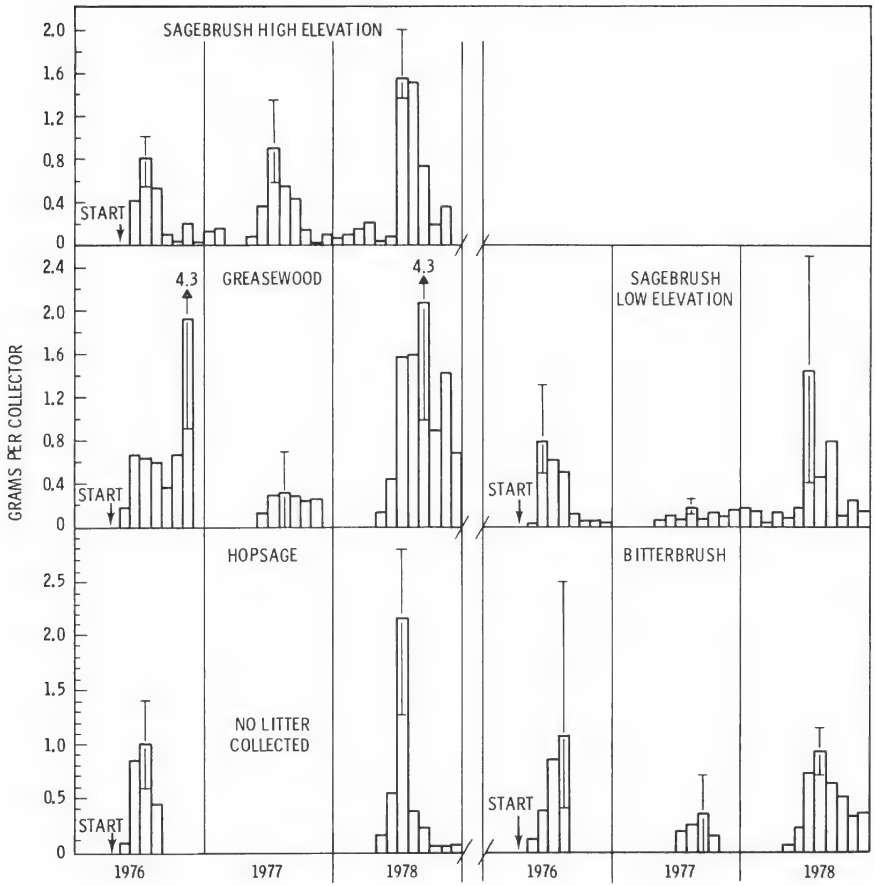


Figure 1. Monthly collection of shrub litterfall on the Arid Lands Ecology Reserve in the growing seasons of 1976, 1977, and 1978. The values are means ($n = 4$) and the vertical bars are extremes of the month of peak litterfall.

son in the shrub steppe region and clearly shows that 1977 was extremely dry (Fig. 2). Only 5 cm of precipitation was recorded at the two lower elevation sites and 7.3 cm at the high elevation site. The 1978 growing season was much wetter than the 1976 season, with 25.4 cm of precipitation recorded at the high elevation site, 18.8 cm at the low elevation sagebrush site, and 15.3 cm at the greasewood-hopsage site (Fig. 2).

These data show that monthly collections of shrub litterfall is a way to monitor the leaf growth of steppe shrubs. Growth of shrubs as measured by the amount of collected litterfall was relatively small in the drought year of 1977 at all sites except the high elevation sagebrush site. Hopsage failed to produce leaves in 1977. However, leaf growth for all plants was restored in the 1978 season when precipitation was more normal. The moderate response of the high elevation sagebrush plants to the 1977

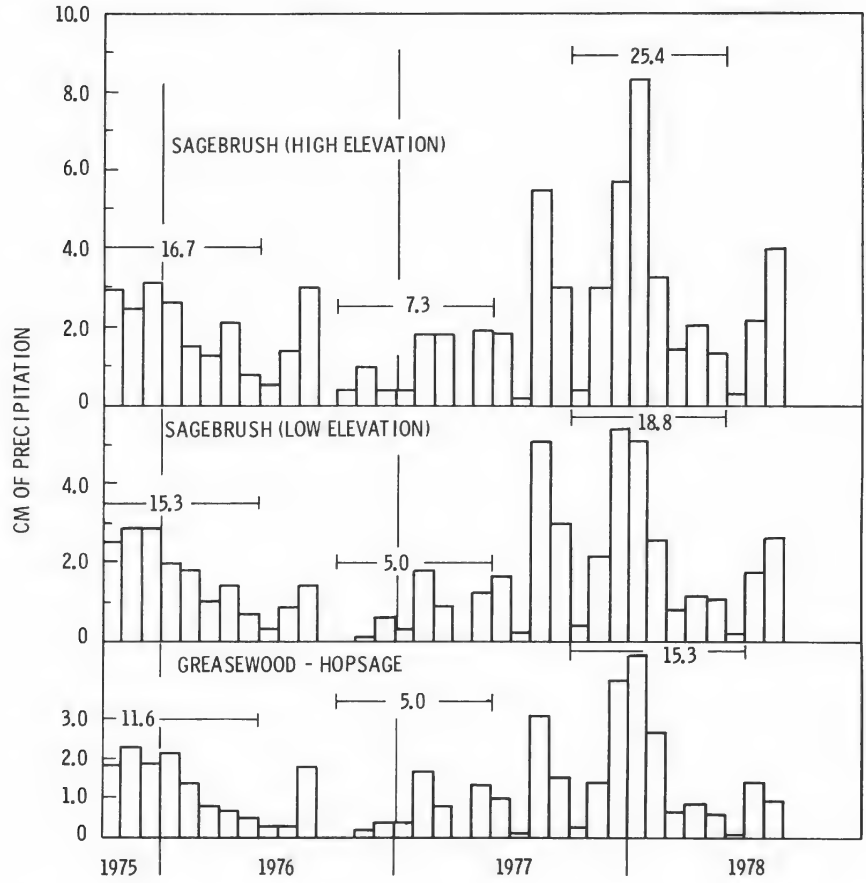


Figure 2. Monthly precipitation (cm) measured at three litterfall collection sites during the growing seasons of 1976, 1977, and 1978. The numerical values show the amount of growing season precipitation October through May.

drought is unexpected. Snow drifts are deposited at this site and the soil water regime may be more mesic than the rain gauge indicates.

There are factors other than weather that can influence litterfall collections. Insects can defoliate shrubs. The moth, *Aroga websterii*, has been known to defoliate and kill *Artemisia* shrubs (Gates, 1964). Grasshoppers also forage upon shrub leaves (Sheldon and Rogers, 1978). Mule deer, *Odocoileus hemionus*, browse upon steppe shrubs, especially bitterbrush. However, mule deer are scarce at the bitterbrush site studied, and there was no evidence that bitterbrush plants were being utilized by deer. Jackrabbits are widespread throughout the shrub steppe vegetation, and they also eat shrub leaves (Uresk, 1978). There was no indication that insects or vertebrate animal foraging were important factors in limiting litterfall collections during the period of this study.

Herbicide damage to shrubs can occur even at great distances from the point of application from leakage en route from airport and field; so, too, small droplets may remain aloft long enough to drift away from the target field. The sites selected for study are remote from agricultural fields and are probably not exposed to herbicide drift from aerial applications.

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# Laboratory Studies of *Chaoborus* Predation on Zooplankton

**Abstract**

Fourth instar *Chaoborus americanus* larvae were fed in the laboratory for over two years, during which time the larvae ate an average of 1.61 prey animals each per day. One larva lived and ate actively in culture for 743 days. Most of the larvae pupated, and several of the pupae emerged successfully. Changes in food supply, temperature, or light seemed to have little effect on the initiation of pupation. In the experiments, prey were offered in different size categories, quantities, and species combinations to determine food preferences. Within the 0.7 mm to 1.8 mm range, there was little evidence of selection for size. Selection of diaptomid over cyclopoid copepods was probably linked to behavior rather than to size or food quality. Temperature seemed to have the greatest effect on feeding rates.

## Introduction

To obtain data for estimating the ecological efficiency of invertebrate predators in lakes and for assessing the potential impact of their predation on the zooplankton, it is useful to conduct laboratory feeding studies to complement field studies. Data on feeding rates and food selection for *Chaoborus* species are not abundant and, although many studies suggest a broad menu and range of feeding rates for these predators, the need for detailed studies has often been expressed (e.g., Parma, 1969, 1971). For instance, the role of rotifers in the *Chaoborus* diet is not completely clear, although it seems likely that they are most important in the first three instars (Lewis, 1975; Parma, 1971).

The assessment of feeding rates and food selection has often been based on crop examination in *Chaoborus* (e.g., Lewis, 1975; Swift and Fedorenko, 1973). Not many *in situ* studies have been conducted using cages or similar devices (e.g., Dodson, 1974) and, although important, such field studies are difficult to maintain over long periods. Consequently, most studies have been done in the laboratory, and many of these lasted no more than 24 h (Dodson, 1970; Swüste, Cremer, and Parma, 1973) or a few days (Allan, 1973). The possibility of a rather long life span for some *Chaoborus* species, especially those adapted to cold waters, adds an extra dimension of difficulty to the maintenance of long-term laboratory cultures. The generation time for some species of *Chaoborus* is reported to be quite short; larvae remain in the fourth instar for only three or four weeks (Lewis, 1975; Parma, 1971); but other species show that the larvae may overwinter in the fourth instar and that the total life span may be at least two years (Fedorenko and Swift, 1972).

In the present study, predation rates and aspects of food organism preference by fourth instars of *Chaoborus* were examined frequently on the same experimental animals for over two years. This work represents the conclusion of some laboratory and field studies begun earlier (Anderson and Raasveldt, 1974).

## Methods

Laboratory methods were essentially the same as those summarized by Anderson and Raasveldt (1974). Individual fourth instar *Chaoborus americanus* (Johannsen) larvae from Herbert Pond (Anderson, 1974) were kept in glass jars containing approximately 65 ml water from the pond. The jars were kept in a controlled-temperature water bath. Regular renewal of the water in the jars was stopped because the predators seemed to suffer more stress from the change than from the old water. One animal fed actively and appeared to be completely healthy for over two years, an indication that the conditions in the jars were healthful and probably comparable to those in the pond, where the water renewal rate is very low. Enough water was added with new prey organisms to maintain the water level in the jars. Dead prey, faecal material, and other debris were removed from each jar before new prey were added.

A light-dark cycle of subdued light diffused through a translucent plastic pane was maintained close to the actual day-night cycle for Herbert Pond. On one or two occasions, day length and light intensity were greatly increased or decreased for a short time to see if the change would alter feeding rates or stimulate pupation. These changes semed to have no effect, and no additional experiments with varying light conditions were tried.

The mean observation and feeding interval over all experiments was 4.2 days. Excluding the very long observation periods on the last surviving predator near the end of the experiments, the overall interval was 3.75 days. For the first 340 days, the mean interval was 2.56 days; after day 340, the mean interval was 7.36 days. The prey density at the start of each observation and feeding interval is given in the results. Sometimes prey organisms were not available in sufficient quantities or diversity to keep all experiments going simultaneously at desired concentrations, as evidenced by the gaps in some tables. However, the animals in these experiments were maintained at food levels above basic requirements.

For comparative studies within the overall experiments, certain predators were fed with different prey species, separately or simultaneously, and at varying prey densities. After a period of time, conditions were usually reversed within subgroups under comparison, so that available food was approximately the same for all predators over the long term.

Prey animals used were obtained from many different lakes or ponds during the course of the experiments. No unusual mortality due to changes in temperature or water conditions was noted. The main prey species used were: *Diacyclops thomasi* (Forbes, 1882, emend. Kiefer, 1978), sometimes substituted by similar-sized *Orthocyclops modestus* (Herrick, 1883)—usual rostrum-to-ramus body length 0.8 to 1.0 mm; *Diaptomus sicilis* Forbes, 1882, occasionally substituted by *Diaptomus tyrrelli* Poppe, 1888—usual rostrum-to-ramus body length 1.1 to 1.2 mm; *Aglaodiaptomus leptopus* Forbes, 1882—usual rostrum-to-ramus body length 1.5 to 1.7 mm; *Hesperodiaptomus nevadensis* (Light, 1938)— usual rostrum-to-ramus body length 2.4 to 2.8 mm; *Daphnia pulicaria* Forbes, 1893 emend. Hrbáček, 1959—head-plus-valve body length in three ranges: 0.7 to 1.0 mm; 1.1 to 1.3 mm; 1.8 to 2.4 mm; unidentified dipteran larvae from Herbert Pond—total length $< 3.0$ mm. When *Diacyclops thomasi* and *Diaptomus sicilis* (and occasionally *Daphnia pulicaria*) were fed simultaneously to *Chaoborus*

larvae, prey were selected to minimize size differences (i.e., upper end of the cyclopoid range, and lower end of the diaptomid range).

### Results and Discussion

The mean feeding rates for all predators in the experiments are summarized in Table 1. The mean daily predation rate for all *Chaoborus* larvae throughout the experiment was 1.61 prey animals per predator per day. The predators were subgrouped in various ways to determine whether there were significant differences between animals about to pupate and the group as a whole; between animals successfully emerging and those not emerging; and between the final 50 days of feeding versus the whole experimental period. Predators emerging in less than 100 days from the start of experiments fed at significantly higher rates than the group as a whole. Rates during the final 50 days for all pupating animals were not significantly different from the group as a whole, but were significantly higher than for non-pupating animals. Rates for successfully emerging animals were nearly twice the rates for non-emerging animals during the final 50 days of feeding for each animal considered separately.

TABLE 1. Summary* of mean predation rates during the entire experimental period for 23 fourth instar **Chaoborus americanus** larvae, subgrouped in various ways.

| Subgrouping of predators | N | $\bar{t}$ | SD | $\overline{P_e}$ | SD | variance | Significantly different (or **not****) from: |
|---|---|---|---|---|---|---|---|
| A All predators for the duration of the experiments | 23 | 326.3 | 215 | 1.61 | .606 | .367 | C ($P<0.01$) |
| B All predators living over 100 days in the experiments | 16 | 446.6 | 132 | 1.31 | .297 | .088 | C ($P<0.01$) |
| C All predators emerging in less than 100 days | 5 | 49.0 | 12 | 2.57 | .417 | .174 | A ($P<0.01$) |
| D Last 50 days of feeding for all predators | 23 | — | — | 1.69 | .655 | .429 | G ($P<0.02$)<br>E ($P<0.05$)** |
| E Last 50 days of feeding for all pupating animals | 14 | — | — | 1.96 | .654 | .428 | F ($P<0.01$)<br>D ($P<0.05$)** |
| F Last 50 days of feeding for all nonpupating animals | 9 | — | — | 1.26 | .384 | .148 | E ($P<0.01$) |
| G Last 50 days of feeding for all emerging animals | 6 | — | — | 2.44 | .482 | .232 | D ($P<0.02$)<br>H ($P<0.01$) |
| H Last 50 days of feeding for all nonemerging animals | 17 | — | — | 1.42 | .478 | .228 | G ($P<0.01$) |

*N = no. of experiments in subgroup.
$\bar{t}$ = mean duration of experiments in days.
$\overline{P_e}$ = mean no. prey consumed per predator per day.

Of the 14 larvae which pupated, seven pupated in the September-November period, five in the May-July period, and one each in January and April. Five of six successful emergences were in October-November, and one was in June.

Temperature conditions throughout the experiments and the number of predators in the experiments at a given time are summarized in Figure 1. The mean rates of predation for all animals feeding during periods of consistent temperature conditions, and estimates of the fraction of available prey animals eaten during these periods, were calculated from the raw data sheets and are also summarized in Figure 1. There were highly significant correlations between ambient temperatures and predation rates and between predation rates and the fraction of available prey consumed.

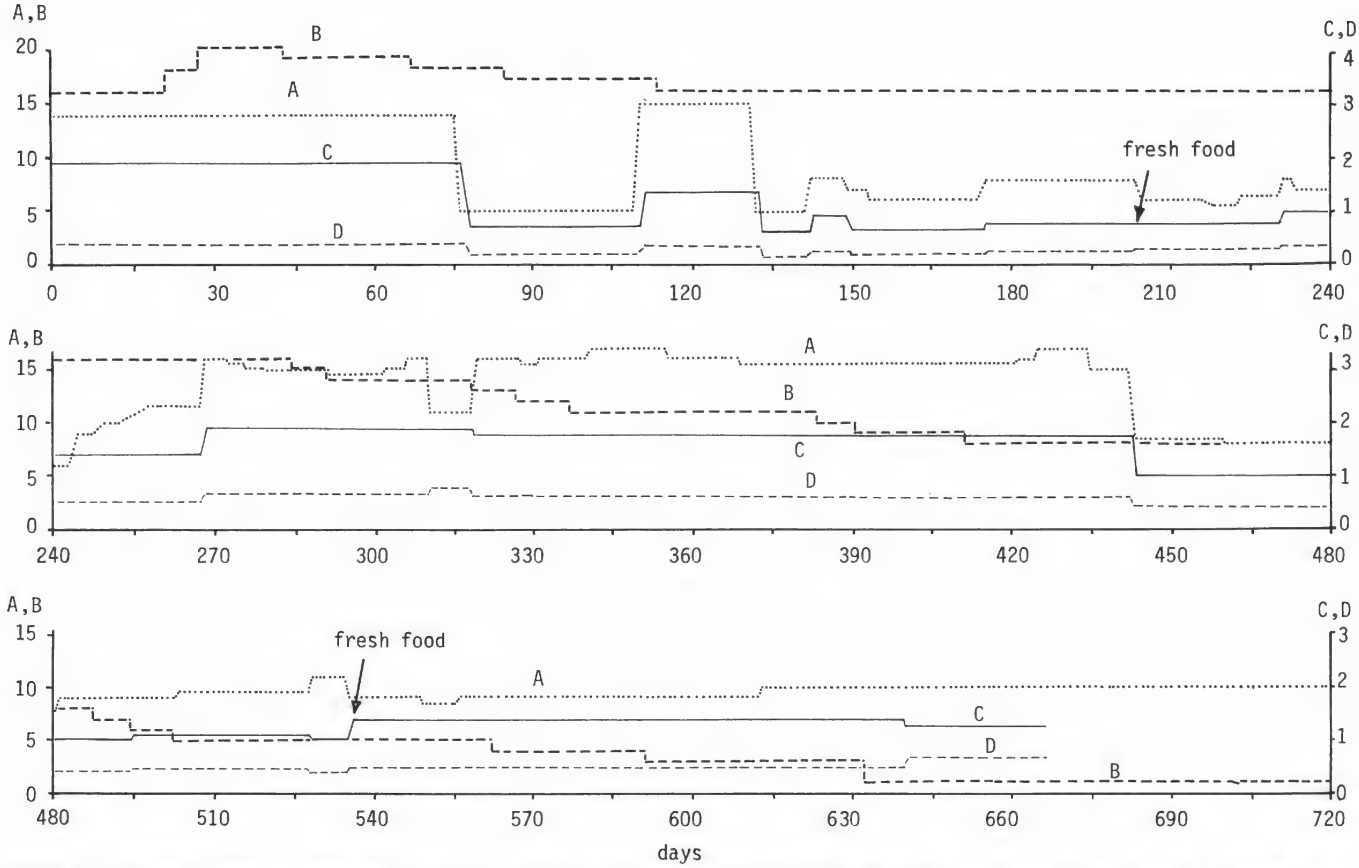


Figure 1. Summary of water temperature (A, in °C); number of animals in the experiments (B); mean daily rates of prey eaten per predator during constant temperature intervals (C); and fraction of available prey eaten per animal during these intervals (D). Correlations between A and C ($r = 0.847$) and between C and D ($r = 0.874$) were significant at the 1 percent level.

The results of comparative studies within the overall experiment are summarized in Tables 2-7 and will be treated in detail in the following discussion.

TABLE 2. **Chaoborus** daily predation rates on **Diaptomus sicilis** adults at different prey densities and different temperatures.♯

| Individual predators (by Lab. No.) | t = 33 days (76 to 109) @ 5°C | | | t = 36 days (109 to 145) @ 15°C | | |
|---|---|---|---|---|---|---|
| | N | $P_a$ | $\overline{P}_c$ | N | $P_a$ | $\overline{P}_c$ |
| 1, 3 | 2 | 5 | 0.50 | 2 | 5 | 0.90 |
| 4, 6, 7, 9, 10, 12 | 6 | 10 | 0.49 | 6 | 10 | 0.86 |
| 13, 14 | 2 | 15 | 0.39 | 2 | 15 | 0.88 |

♯Explanation of column symbols, Tables 2 to 7:
t = duration of experiments in days (day nos. as in Figure 1).
N = no. of experiments in set.
$P_a$ = no. of prey available to each predator.
$\overline{P}_c$ = mean no. prey consumed per predator per day.

Various experiments indicated that the *Chaoborus americanus* fourth instar larvae may live for two years or more and feed continuously at temperatures from 5°C to 16°C. Fedorenko and Swift (1972) suggest a one-year life span for *C. americanus* in Eunice Lake, British Columbia, although a two-year span was possible for *C. trivittatus*. My experiments indicate that a two- or three-year life span for *C. americanus* may occur in cold waters, a possibility supported as well by the year-round occurrence of active fourth instar larvae in many montane and subalpine waters. Also, these experiments tend to confirm Parma's (1971) observations that emergence of *Chaoborus* in culture is possible, although difficult to obtain.

### Predation Rates and Individual Differences

The mean overall rates of predation for the 23 *Chaoborus americanus* fourth instar larvae throughout the entire experiment showed rather little variance at 1.61 prey eaten per predator per day, a rate in general agreement with rates postulated by Dodson (1970) and obtained from short-term experiments by Allan (1973). The variance was even smaller when the total group of predators was split into sub-groups of those which emerged and those which did not. Extremely high rates occasionally noted in the literature (e.g., Deonier, cited by Parma, 1971) may result from experiments which are too short, or to a sudden change in the type or abundance of food, especially if the experiments follow a period of starvation.

My results indicate that an average fourth instar of *C. americanus* could consume about 1200 crustacean plankton prey in two years, and that abundant chaoborid larvae in a lake could be an important control over crustacean plankton abundance as suggested by Allan (1973) and Dodson (1974). Predation in spring by overwintering chaoborid larvae would be an especially important control over the development of certain diaptomid copepod populations.

The mean prey/predator rates during short intervals within the overall experiment usually showed a marked consistency. For example, the mean rates for four individuals for two different intervals are summarized in Table 3; such results were fairly typical. Occasionally, some predators tended to eat less during one interval and more at another (e.g., predator nos. 4 and 6, Table 4, usually ate less at 6° to 8°C, but ate more at higher temperatures, Tables 4 and 7). Predator nos. 4 and 6 were unlikely to be at different

TABLE 3. **Chaoborus** daily predation rates on **Diaptomus sicilis** (Ds) 5th and 6th copepodids (C5 and C6) and **Diacyclops thomasi** (Ct) C4 to C6 fed simultaneously and at different prey densities and temperatures.‡

| Individual predators (by Lab. No.) | t = 47 days (118 to 165) (16 days @ 15°C, 31 @ 5-6°C) N | $P_a$ | $\overline{P_c}$ | t = 84 days (165 to 249) @ 6 to 7°C N | $P_a$ | $\overline{P_c}$ | t= 22 days (249 to 271) @ 11.5 to 15°C N | $P_a$ | $\overline{P_c}$ |
|---|---|---|---|---|---|---|---|---|---|
| 17, 18, 19, 20 | | 5 Ds | 0.71* | | 4 Ds | 0.40** | | 5 Ds | 1.09 |
| (and 23 for last set only) | 4 | | | 4 | | | 5 | | |
| | | 5 Ct | 0.57* | | 6 Ct | 0.41** | | 5 Ct | 0.95 |
| Totals | | 10 Ds+Ct | 1.28 | | 9 Ds+Ct | 0.81 | | 10 Ds+Ct | 2.04 |

*prey of each species consumed per individual predator: Pred. No. 17, 18, 19, 20
Ds = 39, 29, 43, 22
Ct = 36, 26, 31, 14

**prey of each species consumed per individual predator:
Ds = 33, 37, 34, 30
Ct = 42, 28, 26, 41

‡column symbols as in Table 2.

TABLE 4. **Chaoborus** daily predation rates on **Diaptomus sicilis** (Ds) C5 and C6 and **Diacyclops thomasi*** (Ct) C4 to C6 fed separately and simultaneously at different prey densities and temperatures.‡

| Individual predators (by Lab. No.) | t = 18 days (147 to 165) @ 6°C N | $P_a$ | $\overline{P_c}$ | t = 23 days (165 to 188) @ 8°C N | $P_a$ | $\overline{P_c}$ | t = 12 days (189 to 202) @ 6°C N | $P_a$ | $\overline{P_c}$ |
|---|---|---|---|---|---|---|---|---|---|
| 1, 3 | 2 | 5 Ds | 0.97 | 2 | 5 Ct | 0.37 | — | — | — |
| 4, 6 | 2 | 10 Ds | 0.44 | 2 | 10 Ct | 0.41 | — | — | — |
| 7, 9, 10, 12 | 4 | 10 Ct | 0.58 | 4 | 10 Ds | 0.71 | 4 | 2 Ds | 0.21 |
| 13, 14 | 2 | 10 Ct | 0.44 | 2 | 10 Ct | 0.76 | 2 | 2 Ct | 0.21 |
| | | 5 Ds | 1.06 | | 5 Ds | 1.30 | | 5 Ds | 0.33 |
| 15 | 1 | 5 Ct | 0.06 | 1 | 5 Ct | 0.52 | 1 | 5 Ct | 0.50 |
| | | 10 Ds+Ct | 1.12 | | 10 Ds+Ct | 1.82 | | 10 Ds+Ct | 0.83 |
| | t = 18 days (193 to 211) | | | t = 24 days (211 to 235) | | | t = 45 days (235 to 281) | | |
| Individual predators | @ 6 to 7°C | | | @ 7 to 8°C | | | @ 11.5 to 15°C | | |
| (by Lab. No.) | N | $P_a$ | $\overline{P_c}$ | N | $P_a$ | $\overline{P_c}$ | N | $P_a$ | $\overline{P_c}$ |
| 1, 3 | 2 | 5 Ct | 1.19 | 2 | 10 Ct | 1.23 | 2 | 10 Ct* | 1.86 |
| 4, 6 | 2 | 10 Ct | 0.61 | 2 | 5 Ct | 0.69 | 2 | 10 Ct* | 1.98 |
| 1, 3, 4, 6 (total) | — | — | — | — | — | — | 4 | 10 Ct* | 1.92 |
| | | | | t = 33 days (204 to 237) | | | t = 44 days (237 to 281) | | |
| 7, 9, 10, 12 | — | — | — | 4 | 5 Ds | 0.60 | **4** | **10 Ds** | **1.30** |
| 13, 14 | — | — | — | 2 | 5 Ct | 0.68 | 2 | 5 Ct* | 0.97 |
| | | | | | | | | 5 Ds | 0.91 |
| 15 | — | — | — | — | — | — | 1 | 5 Ct | 0.36 |
| | | | | | | | | 10 Ds+Ct | 1.27 |

*Prey changed from **D. thomasi** to **Orthocyclops modestus** on day 267 for a few days with no apparent change in predation rates.
‡Column symbols as in Table 2.

TABLE 5. **Chaoborus** daily predation rates on **Aglaodiaptomus leptopus** C5 and C6 at different prey densities.‡

| Individual predators (by Lab. No.) | t = 22 days (42 to 64) @ 14°C N | $P_a$ | $\overline{P_c}$ |
|---|---|---|---|
| 1, 2, 3 | 3 | 5 | 1.44 |
| 7, 9 | 2 | 10 | 1.33 |
| 13, 14 | 2 | 15 | 1.00 |

‡Column symbols as in Table 2.

TABLE 6. **Chaoborus** daily predation rates on **Diaptomus sicilis** (Ds) C5 and C6 and **Diacyclops thomasi** (Ct) C4 and C5 fed separately and simultaneously.‡

| Individual predators (by Lab. No.) | t = 18 days (14 to 32) @ 14°C N | $P_a$ | $\overline{P_c}$ |
|---|---|---|---|
| 1, 2, 3, 7, 8, 9, 13, 14 | 8 | 20 Ct | 6.03 |
| 4, 5, 6, 10, 11, 12 | 6 | 10 Ds | 3.28 |
| | | 20 Ct | 1.36 |
| 15, 16 | 2 | 10 Ds | 1.64 |
| | | 30 Ds+Ct | 3.00 |

‡Column symbols as in Table 2.

TABLE 7. **Chaoborus** daily predation rates on **Daphnia pulicaria** (Dp) with other prey (Ds and Ct, as in Tables 3, 4, and 6) and small dipteran larvae (dL).‡

| Individual predators (by Lab. No.) | t | Temperature | N | $P_a$ | $\overline{P_c}$ |
|---|---|---|---|---|---|
| | | | | 2 DS | 0.42 |
| 19, 10 | 51 days (65 to 116) | 5°C | 2 | 4 Dp (2L, 2s)* | 0.62 |
| | | | | 6 Ds+DP | 1.04 |
| | | | | 5 Dp (med.) | 0.80 |
| 17, 18 | 63 days (0 to 63) | 14°C | 2 | 1 dL | 0.02 |
| | | | | 6 Dp+dL | 0.82 |
| | | | | 9.5 Ds | 0.46 |
| 13, 17, 23 | 35 days (540 to 575) | 9°C | 3 | 10 Ct | 0.21 |
| | | | | 6 Dp | 0.49 |
| | | | | 25.5 Ds+Ct+Dp | 1.16 |
| 4, 5, 6 | 60 days (0 to 60) | 14°C | | 1.5 Dp (L) | 0.01 |
| | | | 3 | 10 Ds | 1.84 |
| | | | | 11.5 Dp+Ds | 1.85 |

Slightly more small (s) eaten than large (L), but differences not statistically significant.
‡Column symbols as in Table 2.

stages of development than nos. 1 and 3, to which they were compared, for all lived about the same span in the experiments. Such short-term variations as occurred between these pairs indicate an important potential weakness in experiments of very short duration, however.

The summary in Figure 1 and the raw data suggest no significant decline in predation rates for individual predators or the group as a whole after two years in the experimental chambers. Therefore, a decline in health and vigor with time did not seem to be a factor in the experiments.

The results summarized in Table 1 indicate significantly higher rates of predation in the weeks immediately prior to pupation when ample prey animals were available, especially among animals which eventually emerged successfully. This finding supports Parma's (1969) suggestion that the presence of abundant prey could be a precondition for emergence.

### Frequency of Feeding

Although these experiments were not particularly designed to test the possible effects of different feeding intervals on feeding rates, both the rates summarized in Figure 1 and Table 7, plus an examination of the raw data, suggest that this factor was not an important one within the interval range used here. At similar temperatures, predation rates during the first 340 days (mean interval = 2.56 days) were approximately the same as rates during the days following day 340 (mean interval = 7.36 days).

### Temperature

There was a highly significant correlation between feeding rates and ambient temperatures in the experiments (Fig. 1). The close parallel between feeding rates and the fraction of the total available prey eaten suggests that the effect of temperature is independent of prey density. Tables 2 to 4 indicate more than doubling of feeding rates when the temperature was raised from the 5-8°C range to the 14-16°C range.

The larvae in these experiments showed no ill effects from a large and rapid temperature change, and response was virtually immediate in the changes in predation rates. Figure 1 and a detailed examination of the raw data showed no lag or overshoot in predation rates when temperatures were raised or lowered by 10°C.

### Prey Abundance and Condition

The results in Tables 2, 4, and 5 suggest that there may be an optimum prey density at which feeding rates are highest. In these experiments, rates were usually lower at both high and low densities (i.e., $\geq$ 15 prey/predator and $<$ 5 prey/predator). The low zooplankton densities common to many alpine lakes (Anderson, 1974), coupled with low water temperatures, could act together to contribute to very long generation times for *Chaoborus* species occurring in such lakes.

The condition of prey may be an important factor influencing feeding rates. Occasionally, the sudden input of food freshly collected from a lake appeared to result in slight increases in feeding rates. Twice, the mean rates did not drop as anticipated with a drop in water temperature in the experimental chambers (Fig. 1). In both cases, fresh prey were fed at the time of the temperature change.

### Selection of Prey Species

In a series of parallel experiments in which either *Diacyclops thomasi* or *Diaptomus sicilis* were fed to the *Chaoborus* predators, slightly more *D. sicilis* were eaten, but the difference was not significant (Tables 3, 4, and 6). When the two prey species were offered simultaneously (Tables 4, 6, and 7), *D. sicilis* was usually eaten at a much higher rate. There was no evidence that the cyclopoids had eaten any of the diaptomids. Therefore, the results suggest that prey behavior may be the factor governing selection by the predator. Feeding data given by Lewis (1975) indicate a preference by *Chaoborus* larvae for copepodids over nauplii, but not for diaptomids over cyclopoids.

At the beginning of my experiments, few *Daphnia* were eaten by the predators, but the *Daphina* used were mostly rather large (Table 7). Later, small- and medium-sized *Daphnia* were eaten at approximately the same rates as *Diaptomus sicilis*, although cyclopoids were taken at a lower rate, as noted above. Again, this finding suggests that behavioral differences in the prey may influence selection by the predator. Swüste *et al.*

(1973) and Dodson (1970) suggested no great difference in predation rates on *Daphnia* and *Diaptomus* in short-term experiments, although the first of these authors indicated that initial feeding was heavier on *Daphnia.* On the basis of gut content analysis, Lewis (1975) found a selective preference for cladocerans over copepods, perhaps in part due to behavioral differences at the relatively high temperatures ($>$ 24°C, Frey, 1969) common to Lake Lanao. Allan (1973) also showed higher predation rates for *Chaoborus* on *Daphnia* than on cyclopoids, but suggested that cyclopoids were better at escaping from attacks, even though they were in the size range preferred by the predator. The inability of *Chaoborus* larvae to handle large *Daphnia*, combined with low densities of the latter, may be important in permitting the coexistence of *Chaoborus* sp. and *Daphnia middendorffiana* or other large daphnids in cold mountain lakes.

In one short experiment, small unidentified dipteran larvae and medium-sized *Daphnia* were fed to the chaoborid larvae. Although a few dipteran larvae were eaten, there was a clear preference for *Daphnia* (Table 7).

### Prey Size

In one experiment in which large and small *Daphnia* were offered simultaneously, slightly more small prey were taken, but the difference was not significant (predator nos. 19 and 20, Table 7). In this same group of experiments, predator nos. 13, 17, and 23 obviously did not select the smallest prey (i.e., the cyclopoids), which once again indicates that behavior may be more important than size. These results are in contrast to those of Allan (1973), who recorded a clear preference for smaller prey. In other experiments, *Aglaodiaptomus leptopus* was readily eaten (Table 5), although at lower rates than *Diaptomus sicilis.* The former were much larger than the latter.

In some other experiments not detailed here, *Hesperodiaptomus nevadensis* was not eaten at all by *Chaoborus americanus* larvae, even though they lived together in the experimental jars for several weeks. Dodson (1974) reported that *C. americanus* would eat adults of the closely related *H. shoshone*, although he suggested that the latter were not a common prey under natural conditions.

In other short-term studies within the overall experiment, large and small *Diaptomus sicilis* copepodids were fed to the chaoborid larvae. Although it was not possible to continue the experiment because of the time required to sort prey or because prey of suitable size differences were not available, the slight preference found for the smaller copepodids was unlikely to have been significant. Lewis' (1975) results indicated that the nauplii of both cyclopoids and diaptomids were unimportant in the chaoborid diet in spite of their greater abundance in the plankton. In some circumstances, this occurrence might be due as much to spatial separation as to selection for size, because diaptomid nauplii and early copepodids often concentrate in the epilimnion where temperatures are higher (Culver and Brunskill, 1969; Herzig, Anderson, and Mayhood, 1980).

### Conclusions

There seems to be little or no size selection by *Chaoborus americanus* fourth instar larvae for prey between 0.7 mm and 1.8 mm, although prey larger or smaller than this preferred size range were selected at lower frequencies in long-term experiments. Pre-

dation rates of these larva on zooplankton are highly temperature dependent.

The preference of *C. americanus* fourth instar larvae for diaptomid copepods over cyclopoids, combined with the long life span of the larvae, is likely an important factor limiting diaptomid abundance in some mountain lakes. Active larvae are present in spring when the diaptomids normally reach the copepodid stage. Furthermore, diaptomid copepodids and adults in small mountain lakes (especially species of *Hesperodiaptomus*) may descend to feed on the lake bottom at times (Anderson, 1974 and unpubl. data) when they could be readily available to *Chaoborus* larvae. There is a marked correlation between *Chaoborus* dominance in fishless lakes and the absence or sparseness of species of diaptomids (Anderson, 1980).

A two-year or longer life span for *C. americanus* is likely in cold waters. Such long life spans among species of *Chaoborus* may be more common than suspected. Because so much of the larval period is spent in the fourth instar, it would be best to use larvae that were reared from third to fourth instar to minimize variability in laboratory experiments.

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# Subalpine Parks Associated with Snow Transfer in the Mountains of Northern Idaho and Eastern Washington

**Abstract**

On five widely separated ridges in northern Idaho and adjacent Washington, ecological studies have been made of unforested areas which have resulted from mainly the transfer of snow from windward to leeward slopes. In the rainless summers, soils of the windward slopes dry much more completely than do soils of the regional subalpine forests. Snow accumulating just over the crests of the ridges persists far into summer, and this either prevents the establishment of tree seedlings or stunts and breaks individuals. The flora of the xerophytic parks of windward slopes has strong affinities with the steppe of the basal plain to the west, whereas the snowdrift habitats of the lee slopes contain a preponderance of taxa common at upper timberline, if not in alpine habitats, on higher mountains to the east.

## Introduction

Permanently treeless areas of limited size frequently interrupt the continuity of forests throughout the Rocky Mountains. These areas, long referred to as parks, may be associated with a variety of edaphic or topographic conditions such as poorly aerated soils, avalanche tracks, soils with low water-storage capacity, steep slopes subject to abnormal exposure to wind and sun, or to excess snow accumulation. This account concerns the vegetation of the last two of these categories.

## Literature Review

After pioneer reconnaissance work on the forests in the northern Rocky Mountains, J. B. Leiberg entered these comments in his report of 1899: the southerly faces of high ridges with an east-west trend "may contain expanses of 50-500 acres having but scattered trees and shrubs, but covered with a dense and heavy growth of mountain grasses. Such tracts are areas that were once heavily timbered, but have had their forest burned off, and, owing to direction and angle of slope causing too rapid drainage and evaporation, have been rendered too arid to permit a renewal of forest growth. The only litter on these tracts are the charred stumps of trees consumed by fire centuries ago. The northerly slopes of such ridges usually bear a forest. . . , while the comb of the ridge has a dense, low-growing belt of young subalpine firs bent and twisted in all directions by the weight of the snow that is blown up over the southern face of the ridge." He later attributes the "permanently deforested tracts on the southern slopes . . . to their position above water level, which is the line on any given slope where the seepage from the crest above first comes to the surface. It varies with changes in angle of slope, dip and strike of the strata, fissuring of the rock formation, etc."

Larson (1926) hypothesized the existence of the south-slope parks as simply "the result of repeated fires"; however, Daubenmire (1944) could see no clear evidence that fire has been a major causal factor.

Secor (1960) studied the distribution of volcanic ash in the vicinity of the large park on Gisborne Ridge (treated below), and found that ash deposits are relatively thin on all southerly slopes, whether vegetated by grassland or by subalpine forest.

Daubenmire (1968) presented results of a late-summer analysis of soil moisture in a transect across Gisborne Ridge. The soils proved to be physiologically dry to depths of 20-40 cm "in the *Agropyron-Festuca* park, the subtending fringe of *Prunus* scrub, and the narrow belt of *Pseudotsuga* just below. Soils beneath forests containing *Abies lasiocarpa* showed no soil drouth even at this season of maximum dryness, and even though two of the sites were barely within the forest on either side of the park, one on the exposed crest of the ridge and the other on the south-facing slope below the *Pseudotsuga* fringe. . . . Parks of this nature appear to be due to excess transfer of precipitation from windward to leeward slopes, this transfer during period of snow cover being at maximum where the grasses dominate."

Attention has so far been centered on the environmental causes of these parks, whereas their plant life has not yet been considered.

## Methods

Scores of parks of the above-described character occur in northern Idaho and eastern Washington. Among those visited, five have been selected for consideration in this study (Fig. 1). They are all relatively large in relation to the average size, all are essentially in pristine condition, and they form a series well distributed over the area.

The terminal standing crop of grass-dominated vegetation was estimated by clipping all vasculares at the soil surface in an area 1 x 10 m.

Measurement of three non-adaptive characters of fertile grass tillers (length of blade of first leaf below the spike, length of the peduncle between this blade and the lowest node of the spike whether the latter is sterile or not, and the distance between the first and third nodes at the bottom of the spike) were made on one fertile tiller from each of 30 scattered individuals in a population. Such analyses were made in three parks and at six locations widely scattered on the basal plain in eastern Washington.

### Topography and Soils

The upper edge of the five parks studied varies between 1780 and 1970 m as determined with a small altimeter. Climatic upper timberline at this latitude lies at approximately 2700 m.

The two northernmost parks were glaciated, but their altitude is high enough that ice inundation was probably of short duration. The three southerly parks were definitely unglaciated, although there were mountain glaciers in their immediate neighborhood in late glacial times.

All five ridges present steep slopes facing a southerly direction, but to this character must be added another important topographic feature which determines park environment rather than forest environment. The conformation of the mountainous topography must be such as to concentrate the force of wind, and thus ensure the transfer of much snow and probably some rain as well from windward to leeward slopes. The windward slope usually has a southerly aspect, but it is not invariably so.

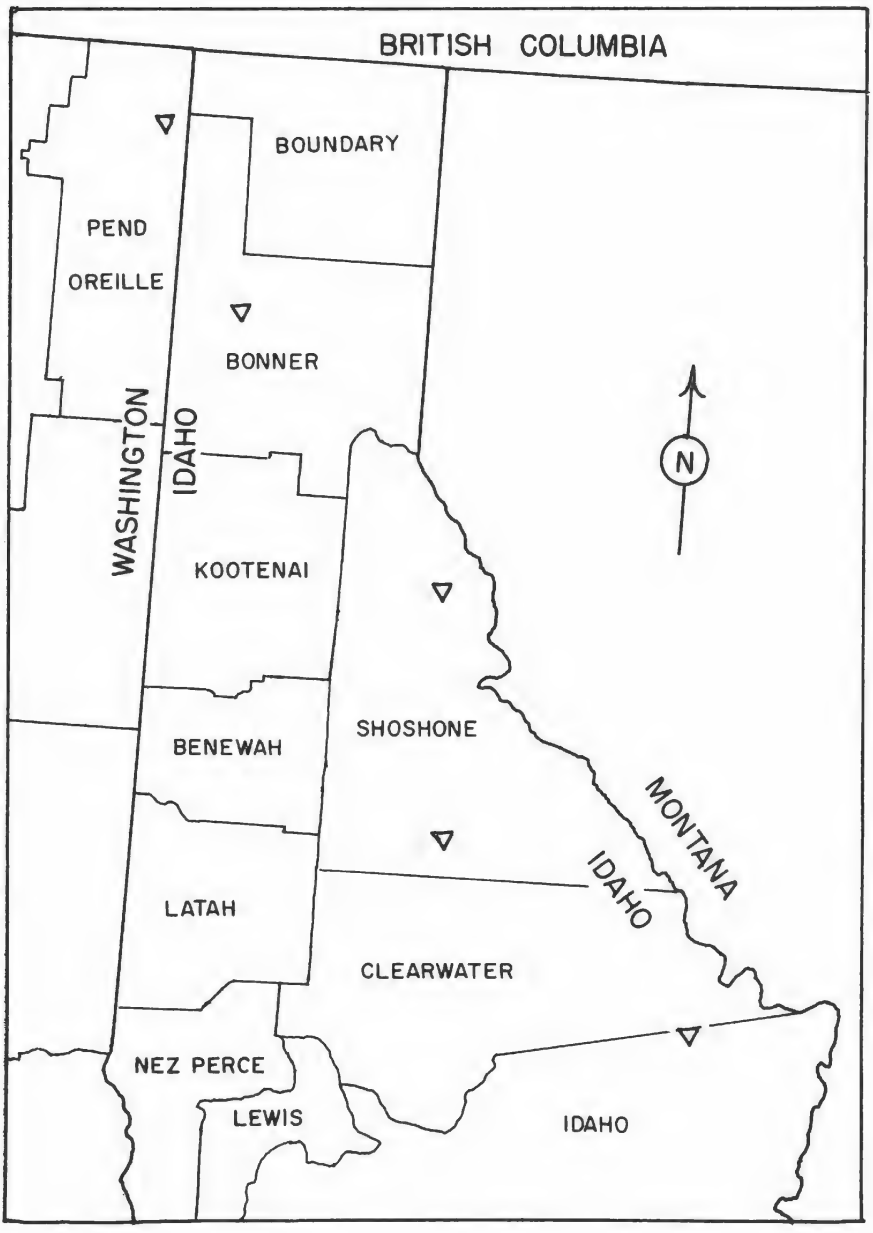


Figure 1. Locations, indicated by triangles, of the five sites studied. From north to south these are: Roundtop, Gisborne Ridge, Grizzly, Freezeout, and Baldy.

The ridges with these parks are forested at the same altitude and on the same aspect on sections where the wind force is less concentrated.

Metamorphosed granitic or sedimentary rocks either outcrop or lie near the surface everywhere, so the mantle of soil is frequently critically thin as well as stony. Where trails cross the deeper soils of south-facing slopes, the soil is so rich in humus that it is easily pulverized during the dry summers and either blows away or is later washed away. Such trails become knee-deep ruts. Even the thin soils are fragile, as indicated by the accumulations of soil by creep on the slope immediately above caespitose perennials, coupled with steep declivities frequently exposing roots on the downhill side. Obviously only light grazing by livestock should be permitted on these grasslands, and the recent incursion of trail cycles will wreak havoc if not stopped.

A remarkable feature that probably originated in late-glacial time is the solifluction lobes of southerly slopes (Fig. 2). On Gisborne Ridge and Bald Mtn. these are asymmetric mounds several meters across, with their steep down-slope margins mostly 0.5-1.5 m high. A long, irregular chain of such mounds follows roughly along a contour on Roundtop. The vegetation of these lobes tends to be distinctive in supporting dense clones of a rhizomatous ecotype of *Agropyron spicatum.* Their soils have relatively low stone content, and rodent activity is if anything less evident in the lobes than in the more stony surrounding soil, and curiously unlike the rodent-ridden mounds on steppe lithosols of the basal plains.

Abundant populations of Columbian ground squirrel and pocket gopher churn

Figure 2. A meter stake stands at the foot of a solifluction lobe covered with rhizomatous *Agropyron spicatum. Hieraceum albertinum* is especially conspicuous in the surrounding community on stony soil. Baldy.

the stony soils and thus augment downslope creep. A badger was once seen on the Gisborne Ridge park, but no diggings of this animal have ever been observed. Possibly the summers are too short to allow this predator to take regular advantage of the bountiful rodent supply.

### Fire

I do not believe fires have been important in determining the existence or size of these parks. The widely scattered trees grow slowly, and when they die their remains decay slowly. Fires appear to sweep nearly every parcel of forest land at intervals seldom longer than 300 years (Daubenmire and Daubenmire, 1968); such fires would certainly spread across at least the drier type of parks. Forest soils commonly contain charcoal, and charred remains of old trees are about as thinly scattered as are old living trees in the parks. There is no evidence that young trees are invading those parks which have not been burned for decades. Finally, the old trees of *Abies lasiocarpa* and *Pinus albicaulis* which dot the dry parks are thin-barked, and would easily have been eliminated had there been much burning.

### Wind and Precipitation Transfer

In the northern Rockies the summers are essentially rainless; most plant growth depends on water stored in the soil during winter precipitation. On the southerly slopes, the reduced reception or retention of precipitation, early melting of a thin snow mantle, and intense exposure to the sun collectively bring about a deep and regular desiccation of the soil.

Although precipitation transfer is by prevailingly southwestern winds, the latter have very little influence on tree form: virtually only *Pseudotsuga* shows some wind training. Winds appear to be strongest in winter when stem tissues are too hardened to be susceptible to permanent deformation, and the wind-driven snow is soft, rather than abrasive like refrozen neve.

Usually the snow blown from southeastern slopes falls just beyond the crests of the ridges and accumulates there as a deep comb (Fig. 3). This accumulation results in a much shortened summer, cold, wet soil, and trees that are either stunted and misshapen (Fig. 4), if indeed they are able to get established.

### Plant Life of the Dry Parks

After reconnaissance, phytosociologic studies of the vegetation of the dry parks seemed so unrewarding that it was discontinued. Apparently, small differences in microrelief affect differences in degree of snow removal or accumulation, with the resulting variation further complicated by differences in drainage, stoniness, depth of soil, direction, and degree of exposure. In contrast with the order that can be made of ecosystem-types in the forests of these mountains, or the steppe below, there is a low degree of repetition of community types here. Only a few generalizations seem warranted.

Extensive clonal patches of *Xerophyllum tenax* occupy irregular areas, and they appear superficially to be pure stands. An absence of stumps, paucity of charred wood, and lack of tree seedlings show that these are not to be interpreted as burned-over remnants of the contiguous *Abies lasiocarpa-Xerophyllum tenax* or *Tsuga mertensiana-Xerophyllum tenax* forest with only the undergrowth persisting.

Figure 3. Dry park with associated snowdrift to the lee of the ridge crest, with camera pointed east. Freezeout, 1 July 1961.

Where the soil is obviously coarse and very stony, communities in which plants such as *Eriogonum umbellatum*, *Arenaria capillaris americana*, *Aster stenomeres*, *Phlox caespitosa*, *Hieraceum albertinum*, etc. form open communities; soil is either bare or moss-covered. Shallow depressions that hold snow and collect meltwater tend to support heavy populations of *Juncus drummondii* or *J. parryi*.

Relatively deep and stone-free loams usually support a community of the highest productivity in which *Festuca viridula*, *F. idahoensis*, and *Agropyron spicatum* are dominant. On Gisborne Ridge, the terminal standing crop of this grass-dominated community proved to be almost equal to the maximum value (368.0 g/m$^2$) ever obtained for the most productive type of steppe vegetation on the basal plain just west of the Bitterroot Mountains (Daubenmire, 1970).

Typically, there is a belt of deciduous shrubbery adjacent to forest along the downslope margin of the dry grassy parks. This heterogeneous belt usually shows *Prunus emarginata*, *Populus tremuloides*, or *Alnus sinuata* as dominant. *Acer glabrum douglasii*, *Sambucus melanocarpa*, and *Sorbus scopulina* are among minor canopy dominants that may be present. Where a spring or seepage originates within a grassy slope, a slender line of *Alnus sinuata* may follow it closely as the ribbon of wet soil extends downslope and enters the forest below.

The widely scattered trees that dot most parks are disfigured by wind breakage and do not attain their genetic potential in terms of stature. Although the *Prunus emarginata* shrubs which dominate the lowest belt of non-forest vegetation on Gisborne Ridge are

Figure 4. An individual of *Abies lasiocarpa* from a snowdrift habitat, with 179 xylem layers at the base of the trunk. Such trees remain sterile unless they eventually reach much greater height. Gisborne Ridge.

conspicuously bent upslope, this feature is more attributable to snow weight than to wind.

In places a small clone of *Abies lasiocarpa* seems to have developed around a previously successful seedling of *Pinus albicaulis*. The essentially symmetrical form of these clones suggests that some microenvironmental influence other than wind protection has favored the late-comers.

The species of trees observed at both the upper and lower margins of dry parks include *Abies lasiocarpa*, *Picea engelmanni*, *Abies grandis*, *Larix occidentalis*, and *Tsuga mertensiana*. *Pinus albicaulis* occurs along the upper margin but not the lower. Pseudotsuga is usually found only along the lower margin.

Typically, the forest on the slope below the dry parks belongs to the *Abies lasiocarpa-Pachistima myrsinites*, or *Tsuga mertensiana-Pachistima myrsinites* association in the classification of Daubenmire and Daubenmire (1968). Southerly slopes at the same elevation as the dry peaks but less exposed to wind support *Abies lasiocarpa-Xerophyllum tenax* or *Tsuga mertensiana-Xerophyllum tenax* forest.

### Origin of the Xerophytic Park Flora

From the numerous disjunct species that are common to both the steppe below lower timberline and the widely separated dry sites high in the mountains (Table 1), one might hypothesize that these taxa were able to penetrate the mountains by ascending exposed ridges when the latter lost most or all of their forest cover during Hypsithermal time. The subsequent cooling trend then enabled trees to reforest most of the ridges, and thus isolate fragments of the grassland peninsulas persisting in the most drouthy spots. Such an hypothesis does not solve the question as to how and when *Eriogonum subalpinum*, *Festuca viridula*, *Aster stenomeres*, *Arenaria capillaris americana*, etc., gained representation in the same high altitude parks, since they do not occur in the steppe to the west.

TABLE 1. Terminal standing crops, as oven-dry g/m², of heavy grass cover on deep humus-rich soil on the south slope of Gisborne Ridge.

| | Plants | g/m² |
|---|---|---|
| Grasses | **Festuca viridula** | 163.9 |
| | **F. idahoensis** | 76.8 |
| | **Agropyron spicatum** | 45.7 |
| Dicots | **Lupinus sulphureus sulphureus** | 38.5 |
| | Others | 7.5 |
| | | 332.4 |

When disjuncts arise by stress that reduces and disrupts a plant's range, this stress may diminish the size of the gene pool in the fragmentary populations by eliminating genetic material which is out of harmony with the new stress, along with any non-adaptive genes that are linked. It therefore seemed worth determining if there was any reduction in genetic variability in the park populations of a species presumed to have arrived through steppe expansion in Hypsithermal time, and *Agropyron spicatum* was selected for such a test. Analysis of the results showed clearly that the magnitude of variability in these characters is approximately equal among the nine populations. In addition, awned and awnless forms are erratically distributed in the dry parks and on the basal plain.

The conclusion supported by the above quantitative analyses is supported by another character, one of adaptive significance. In the park environment, *Agropyron* exhibits the same genetic sorting into ecotypes as in meadow-steppe just below lower timberline, in that only seedlings genetically destined to provide caespitose individuals can survive in open disturbed areas such as roadsides; but these have been replaced by rhizomatous plants in the dense communities of well stabilized areas. Thus, except for a caespitose individual collected along the primitive road that skirts Gisborne Ridge, no difference has been found in subalpine and steppe populations of this grass. The exception was 156 cm tall, and can be seen in the WSU Herbarium. One might conclude that either the

isolation of the park populations has been too recent to have allowed significant sorting of biotypes, or that park environment is too similar to steppe environment to have affected biotype composition.

### Plant Life of the Snowbank Parks

Along the crests of these wind-swept ridges, there is typically a slender and discontinuous strip of forest (Fig. 3) where, in the transition between snow-depleted and snow-enriched topography, snow cover is approximately normal for the subalpine area. Slightly to the lee of this area, drifts sometimes as much as 6 m deep may occur. Since the deepest part of the drift is of small size, there are somewhat concentric zones of diminishing snowdrift influence arranged about it. Fairly distinct aspects of snow influence can often be recognized; for discussion purposes, these aspects will be designated as Aspects I, II, and III.

Aspect I is found where drifts are barely deep enough to cause a recognizable differentiation in the kinds and forms of plants; these drifts have little or no evident influence upon the old trees, but the stems of small individuals as well as those of tall shrubs in the undergrowth are much contorted by the long annual periods of snow accumulation and settling. Sufficient numbers of seedlings are able to outgrow this suppression, or escape its impact by accident of location with respect to large individuals, so that the trees are able to perpetuate themselves in near-normal density. With age, most of the deformity evident in the young trees gradually disappears, presumably due to compensatory cambial growth, so that most of the thick trunks are nearly straight.

*Luzula hitchcockii* is especially predominant in the undergrowth here, although it extends into parts of the forest in which snow accumulation is insufficient to cause the deformation of young trees, as well as into areas of more severe snow influence. The degree to which this herb is physiologically adapted to areas of abnormal snow persistence is indicated by the fact that frequently etiolated shoots have inflorescences grown to nearly full size under the snow—a behavior which largely offsets the effect of delayed spring.

Vegetation of the aspect just described may be the only effect of snow-modification on ridges where drifting is only slight; elsewhere, it forms a transitional zone between unmodified forest and vegetation of Aspect II.

A degree of snow injury distinctly greater than Aspect I may be recognized by the dwarfness and distortion of all trees in the area (Fig. 4). All of them have crooked stems, and the lower branches tend to be relatively short-lived owing at least in part to the abundance of brown felt blight caused by *Herpotrichia nigra* and/or *Neopeckia coulteri*. These fungi parasitize foliage sprays while they are covered with snow, taking advantage of the high humidity and uniformly cool temperatures within the snowdrift.

The greater the height a tree attains in this habitat, the more likely it is to be broken off by snow weight. Individuals seldom reach 2 dm in diameter at breast height before being maimed in this way; the abundance of low, jagged stumps in this dwarfed timber attest to the frequency of the event.

The low evergreen shrubs *Phyllodoce glanduliflora* and *P. empetriformis* are especially abundant in this dwarf timber.

Aspect II in turn surrounds Aspect III, which consists of those habitats in which the deepest and most persistent snowdrifts result in a park in which no trees can become

established. This central treeless area and, to a limited extent, openings between the dwarfed trees which surround it, support a unique flora with species which are very rare if not completely lacking in other habitats on the ridge (see Appendix). Here there are species not otherwise found below alpine timberline. All but a few of the largest snowpatch habitats must have become extinct through tree invasion during Hypsithermal time, as higher temperatures reduced snow depth and persistence. Then with subsequent cooling, the very small sizes of the snow patches which developed provided targets for the disseminules of alpine species that were rarely hit. The distinctiveness of the flora would probably be much more striking but for the constant rain of disseminules of south-slope xerophytes, which introduces species that occasionally germinate and complete most of their life cycles here.

One-fifth of the snowpatch flora consists of plants characteristic of the *Menziesia ferruginea* union that forms the undergrowth of forests just below the snowdrifts.

As indicated earlier, snowdrift vegetation of even Aspect I may be lacking in those areas in which topography favors the wide scattering of blown-over snow rather than its concentration in deep drifts.

### Altitudinal Affinities of the Park Vegetation

Forty-nine percent of the dry park species listed in Table 1 are known to occur below lower timberline on the basal plain to the west. Using Lackschweitz's (1970) list of the alpine and upper timberline flora of the Bitterroots as a base, only 27 percent of the dry park flora extends to upper timberline and alpine environments.

In the snowdrift flora, only 16 percent occur on the basal plain, a value which would shrink considerably if unadapted waifs from windward slopes were ignored. As might be expected, 56 percent of the snowdrift taxa occur at upper timberline or higher.

### Geographic Distinctiveness of the Dry Parks

The information available on subalpine grasslands of surrounding regions indicates that the dry parks of the area represented by the five sites here treated have a significant degree of distinctiveness. These additional distinctions support this assertion. Not far west of Roundtop in eastern Washington, as well as on Mt. Spokane to the south of it, subalpine grasslands begin to include *Artemisia tridentata vaseyana* as a characteristic element. Such parks extend from there westward across the northern tier of counties and also occur on the mountains of southeastern Washington and contiguous Oregon (Strickler, 1961). This shrub is completely absent from the parks described here. Furthermore, *Stipa* is represented well in the *Artemisia*-containing parks, but has not yet been seen in northern Idaho parks.

East of the Idaho parks, including the crest of the Bitterroots and mountains in western Montana, the important grass *Festuca viridula* is absent from montane parks (Root and Habeck, 1972). Also lacking are *Arenaria capillaris americana* and *Senecio integerrimus*, which are regularly conspicuous in northern Idaho.

**Acknowledgments**

I wish to thank Jean B. Daubenmire for general assistance in the field, and Beverly Hunter and Richard Mack for checking certain herbarium records for me.

## Appendix: Park Floras and Their Altitudinal Affinities

The letter *A* follows those taxa also found among the alpine or upper timberline plants by Lackschweitz (1970). *S* designates also in the steppe or ponderosa pine savanna to the west of these parks.

### Windward Parks

*Acer glabrum douglasii* S, *Achillea millefolium lanulosum* A S, *Agastache urticifolium* S, *Agoseris aurantiaca aurantiaca* A, *A. glauca agrestis* S, *A. glauca dasycephala* S, *Agropyron spicatum* S, *Agrostis humilis* A, *A. scabra* A S, *Allium fibrillum* S, *Alnus sinuata, Amelanchier alnifolia pumila* S, *Anaphalis margaritacea, Antennaria rosea* A S, *Apocynum androsaemifolium androsaemifolium* S, *Arabis holboellii retrofracta* S, *A. microphylla* S, *A. nuttallii* A S, *Arenaria capillaris americana* A, *A. congesta cephaloidea* A S, *A. macrophylla, Arnica latifolia latifolia* A, *Artemisia ludoviciana latiloba* S, *Aster foliaceus foliaceus* A, *A. integrifolius* A, *A. modestus, A. stenomeres, Barbarea orthoceros* S, *Berberis repens* S, *Bromus carinatus* S, *Calamagrostis purpurascens, C. rubescens* S, *Calochortus apiculatus, C. elegans selwayensis, Campanula rotundifolia* A S, *Carex geyeri* S, *C. hoodii* S, *C. microptera, C. neurophora, C. rossii* A S, *Castilleja longispica, C. miniata* S, *Claytonia lanceolata lanceolata* A S, *Collinsia parviflora* S, *Cryptogramma achrostichoides* & *crispa* A, *Cystopteris fragilis* A S, *Danthonia intermedia* A S, *Delphinium nuttallianum nuttallianum* A S, *Descurainia richardsonii viscosa* S, *Dodecatheon conjugens* S, *Elymus glaucus glaucus* S, *Epilobium angustifolium* A S, *Erigeron peregrinus calianthemus* A, *Eriogonum flavum piperi* A, *E. umbellatum subalpinum, E. umbellatum umbellatum, Festuca idahoensis* S, *F. viridula* A, *Fragaria* S, *Frasera fastigiata, Galium bifolium, Gayophytum nuttallii* S, *Geranium viscosissimum* S, *Gilia aggregata* S, *Haplopappus carthamoides* S, *Heuchera cylindrica glabella* S, *Hieraceum albertinum* S, *H. gracile* A, *Holodiscus discolor* S, *Hydrophyllum capitatum* S, *Juncus parryi* A, *Koeleria cristata* S, *Ligusticum canbyi, Linanthus septentrionalis* S, *Lithophragma parviflora* S, *Lomatium dissectum multifidum* A S, *Lomatium triternatum triternatum* A S, *Lonicera utahensis, Lupinus argenteus argenteus, L. argenteus depressa, L. caudatus* S, *L. leucophyllus leucophyllus* S, *L. sulphureus subsaccatus* S, *Luzula spicata* A, *Melica bulbosa* S, *M. spectabilis* S, *Menziesia ferruginea, Mertensia paniculata borealis, Microseris nutans* S, *Osmorhiza occidentalis, Pachistima myrsinites, Pedicularis bracteosa bracteosa, P. contorta* A, *P. racemosa, Penstemon attenuatus* A, *Phacelia heterophylla* S, *Phlox caespitosa, P. diffusa longistylis, Phyllodoce empetriformis* A, *Poa pratensis* S, *P. sandbergii* (sensu lata) A S, *Polemonium pulcherrima calycinum* A, *Polygonum douglasii* S, *P. majus* A S, *P. phytolaccaefolium* A, *Populus tremuloides* S, *Prunus emarginata* S, *P. virginiana melanocarpa* S, *Rumex acetosella* S, *Sambucus melanocarpa, Sedum stenopetalum* S, *Selaginella watsoni* S, *Senecio integerrimus exaltatus* A S, *Silene oregana* S, *S. scouleri* S, *Sorbus scopulina scopulina, Spergularia rubra* S, *Spiraea betulifolia* S, *S. densiflora, Synthyris missurica, Taraxacum officinale* A S, *Thalictrum occidentale, Thlaspi fendleri glaucum* A, *Trisetum spicatum* A, *Vaccinium membranaceum, V. myrtillus, V. scoparium* A, *Valeriana sitchensis* A, *Xerophyllum tenax* A, *Zigadenus venenosus* S.

### Leeward Parks

*Achillea millefolium lanulosum* A S, *Agrostis humilis* A, *Antennaria alpina* A, *A. lanata* A, *Arabis lyallii* A, *Arnica latifolia latifolia* A, *Athyrium americanum, Carex mertensiana, C. nigricans* A, *Castilleja miniata* S, *C. rhexifolia* A, *Claytonia lanceolata lanceolata* A S, *Cryptogramma achrostichoides* & *crispa* A, *Deschampsia atropurpurea* A, *Elymus glaucus glaucus* S, *Epilobium alpinum lactiflorum, Erigeron peregrinus calianthemus* A, *Erythronium grandiflorum* A S, *Festuca idahoensis* S, *F. viridula A, Frasera fastigiata, Hieraceum albertinum* S, *H. gracile* A, *Juncus drummondii* A, *J. parryi* A, *Ligusticum canbyi, Lomatium sandbergii, L. triternatum triternatum* A S, *Lonicera utahensis, Lupinus argenteus depressa, L. caudatus* S, *L. sulphureus subsaccatus* S, *Luzula hitchcockii* A, *Menziesia ferruginea, Mitella breweri, Pedicularis bracteosa bracteosa, P. contorta* A, *Penstemon ellipticus* A, *Phlox diffusa longistylis, Phyllodoce empetriformis* A, *P. glandulosa* A, *Polemonium pulcherrima calycinum* A, *Polygonum bistortoides* A, *P. phytolaccaefolium* A, *Ranunculus escholtzii suskdorfii* A, *Rhododendron albiflorum, Rubus parviflorus, Saxifraga ferruginea* A, *Senecio integerrimus exaltatus* A S, *Sibbaldia procumbens* A, *Spiraea densiflora, Thlaspi fendleri glaucum* A, *Vaccinium membranaceum, Valeriana sitchensis* A, *Veratrum viride* A, *Veronica cusickii* A, *Xerophyllum tenax* A.

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# Observations of Fish on and around an Artificial Reef in Puget Sound, Washington

## Abstract

This report describes an artificial reef constructed of large rocks in central Puget Sound, and the use thereof by fish from scuba diving observations. The study was conducted from 1961 to 1969; surveys were made before and after the reef was constructed, both on and adjacent to the reef. Collected data show the species that use the reef, indicate their seasonal occurrence, relate the behavior of fish to the reef, and analyze physical features that attract fish to the reef.

## Introduction

Artificial reefs are known to increase the profusion of marine flora and fauna, and of fish in particular (Stroud and Massmann, 1966; Turner *et al.*, 1969). In the Washington area, man-created physical structures such as pilings, riprap, or sunken vessels, for example, have been noted for their increased biomass of fishes ever since scuba diving became popular in the 1950s. In recent years, several artificial reefs have been constructed by personnel of the Washington State Parks and Recreation Commission (Patten and Mitsuoka, 1972) and other organizations. Some artificial reefs have been studied to estimate their usage by marine life (Patten, 1973, 1976; Walton, 1979). The increase in abundance of marine life on and around the artificial reefs is generally astoundingly apparent; great numbers of species live on and around the physical reef structures whereas few organisms are evident even short distances away, over sand to cobble bottoms. Because there is little understanding of artificial habitat attracting and supporting life in the Washington area, promoters are hard pressed to demonstrate the fishery catch and recreational value of reefs. The study presented here demonstrates the effectiveness of a small artificial reef of rocks in shallow water for attracting fish.

## Description of Study Area

The study area was at Zenith, a community on the east shore of Puget Sound, 25 km south of Seattle, Washington. The site has a gradually sloping bottom (roughly a 5 percent grade) to depths of at least 18 m. Depths were gauged from 0 as determined from the mean of the daily lower low tide, where tidal extremes range from +3.9 to −1.2 m. The bottom is covered with sand or gravel and rocks; some boulders are about 2 m in dimension. The bottom is rocky from the high tide extreme to the 0.5 m depth, sandy from 0.5 to 2.0 m, rocky from 2.0 to 2.8 m, and sandy beyond 2.8 m. Eelgrass (*Zostera* spp.) is abundant in patches in sandy areas 0 to 2 m deep. Algae start growing in March and are profuse from May to October in rocky areas; stormy weather, however, eliminates most of the algae in winter. Some species of algae form dense thickets

on the bottom, and those with gas bladders extend off the bottom; bull kelp (*Nereocystis lutkeanna*) is prominent above subtidal rocks.

I constructed the reef in 2.8 m of water on the offshore extreme of the rocky bottom area in August 1963. Rocks, 30 to 60 cm in dimension, were taken from the beach and dropped at a predetermined location to form a pile about 1.5 m high with an irregular diameter of about 4 m.

#### Methods of Data Collection

I made observations of fish during 54 scuba dives during the day and three at night from 1961 to 1966. A few dives made in 1968 and 1969 were not included in the study except for behavioral observations on the buffalo sculpin (*Enophrys bison*). Ten dives were made from March 1961 to March 1963 before the reef was constructed; 44 dives were made from August 1963 to February 1966. A night dive was made on 24 April 1965, and two were made on 7 and 18 January 1966. Each dive lasted about 50 min. The distance covered by a dive was 150-250 m before the reef was constructed; after construction, the distance was reduced to 80-100 m. Visibility was generally fair for distances of 2 to 15 m except from about mid-May through July when visibility was often less than a meter. Little effort was made to examine the offshore sandy area where few fish were observed. Observations were made over rocky areas at depths of 1.5 to 2.8 m.

Data collected during a dive consisted of noting the occurrence of species present, estimating their length range, observing their behavior, and enumerating cabezon (*Scorpaenichthys marmoratus*) and copper rockfish (*Sebastes caurinus*). Species of questionable identity were collected and identified in the laboratory. Data are considered comparable for all dives and species although turbidity, abundance of algae cover for the hiding of fish, seasonal behavior of a species, and avoidance of or attraction to a diver by a species of fish varied. Probability of sighting a species of fish during a dive by season was estimated by using the frequency a species was observed during all dives within a season. Species observed on 50 percent or more of the dives are termed common; those sighted less frequently, uncommon. Difficulties of fish observation and enumeration have been recognized by Turner *et al.* (1969); they considered, however, that data from diver observation accurately described fish populations.

My ability to sight or approach a fish varied by season and by species of fish. During May to October, algae are profuse over rocky bottoms and the rockpile, which makes observation of benthic fish difficult. For example, by removing algae (*Laminaria* sp.) lying on the bottom, sculpins of the genus *Artedius* were often exposed. Most species were not alarmed by my presence and some exhibited curiosity; a few species apparently avoided me, maintained a comparatively great distance, or bolted during my approach. Fish difficult to approach were the Pacific herring (*Clupea harengus pallasi*), species of Pacific salmon (*Oncorhynchus spp.*), Pacific sand lance (*Ammodytes hexapterus*), pile perch (*Rhacocheilus vacca*), Pacific staghorn sculpin (*Leptocottus armatus*), and starry flounder (*Platichthys stellatus*); of these, the pile perch was the only species attracted to the rockpile. Certain species were not easily viewed; the sailfin sculpin (*Nautichthys oculofasciatus*), pholids, and rockfishes hid in interstices of rocks, and flatfishes buried themselves under sand.

### Findings

Thirty-eight species of fish were observed—28 before the reef was built and 35 afterwards (Table 1). These have all been reported from the study area (DeLacy *et al.*, 1972). The lingcod (*Ophiodon elongatus*), represented by one fish, was the only fish seen before but not after the reef was built. Fourteen species were observed on the artificial reef and 35 species in adjacent areas. The average number of species observed for all seasons after the reef was constructed was 11 for the reef and 23 for adjacent areas. There was little seasonal difference in total species observed (Table 1). Ratfish (*Hydrolagus coliei*), spiny dogfish (*Squalus acanthias*), and white spotted greenling (*Hexagrammos stelleri*) were observed near the reef and were possibly attracted to it. The few brown rockfish (*S. auriculatus*) and painted greenling (*Oxylebius pictus*) observed were seen exclusively on the reef. The buffalo sculpin was seen guarding egg nests on the reef in March of 1968 and 1969, but it had not used the reef prior to this time. Night dives in spring and winter did not reveal fish on the reef other than those observed during the day. Thus, of the 38 species of fish seen in the study area, 14—and possibly 3 others—used the reef.

The stage of life of the species observed, as determined or estimated from length of fish and examination of some gonads, indicated that in some species juvenile forms were absent or were not observed (Table 1).

#### Seasonal Occurrence of Species

Abundance of fish in the study area tended to follow the seasonal solar intensity cycle; March to May, fish abundance increased; from June to September, abundance was maximal; thereafter, it declined. From December to February, the study area exclusive of the reef was virtually barren of fish life, whereas at least 40 fish were counted on the reef per dive. Despite the fewer species of fish using the reef, the biomass was greater on the reef than in adjacent areas throughout the year. Walton (1979) estimated that fish density averaged four times greater over existing reefs and nine times greater over artificial reef than over a sand bottom in central Puget Sound.

The three night dives in winter and spring showed that fish biomass increased greatly at night in the general study area, but did not increase on the reef. The prominent fish seen at night in winter and spring were young buffalo sculpin, cabezon, English sole (*Parophrys vetulus*), Pacific cod (*Gadus macrocephalus*), roughback sculpin (*Chitonotus pugetensis*), sailfin sculpin, shiner perch (*Cymatogaster aggregata*), Pacific staghorn sculpin, and the white spotted greenling. All of these species were few or absent from the study area during daylight hours. The only nocturnally active species seen using the reef in the winter were the cabezon and sailfin sculpin.

Seasonal occurrence of the cabezon, copper rockfish, and striped seaperch (*Embiotoca lateralis*) are given in detail because these species were estimated to constitute the bulk of the fish biomass in the study area and are those most important to fishermen. Shiner perch are also discussed because of their high abundance. Observation of catches of the commercial beach seine fishery for pile perch in the general study area suggests that this species may have been as numerous as the striped seaperch, even though few pile perch were seen.

The striped seaperch was the dominant fish observed in the study area in number and biomass. From June to August, "thousands" of individuals of this species were pres-

TABLE 1. Species of fish observed by season on the reef and near the site of the reef before and after it was constructed.

| Name | Stage of life[1] | Estimated body length (cm) | Seasonal occurrence[2, 3] Near the site of the reef: Before reef was constructed Spring through winter | Near the site of the reef: After reef was constructed Spring | Summer | Fall | Winter | On the reef: Spring | Summer | Fall | Winter |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Big skate **Raja binoculata** | A | 80-110 | U | — | — | U | — | — | — | — | — |
| Black rockfish **Sebastes melanops** | J | 10-28 | — | — | — | — | U | — | — | U | — |
| Brown rockfish **Sebastes auriculatus** | J | 18 | — | — | — | — | — | — | — | — | U |
| Buffalo sculpin **Enophrys bison** | J-A | 9-26 | C | C | C | C | C | — | — | — | U |
| Cabezon **Scorpaenichthys marmoratus** | A | 30-70 | C | C | C | C | C | C | C | C | C |
| Chinook salmon **Oncorhynchus tshawytscha** | J | 18 | U | — | — | U | — | — | — | — | — |
| C-O sole **Pleuronichthys coenosus** | A | 20-30 | C | C | C | C | C | — | — | — | — |
| Copper rockfish **Sebastes caurinus** | J-A | 7-47 | U | U | C | C | U | C | C | C | C |
| Crescent gunnel **Pholis laeta** | X | 15 | — | — | — | U | — | — | — | — | — |
| English sole **Parophrys vetulus** | A | 23-30 | U | U | U | U | U | — | — | — | — |
| Grunt sculpin **Rhamphocottus richardsoni** | X | 5 | — | U | — | — | — | — | — | — | — |
| Kelp greenling **Hexagrammos decagrammus** | A | 35 | U | — | — | U | — | — | — | — | — |
| Lingcod **Ophiodon elongatus** | A | 90 | U | — | — | — | — | — | — | — | — |
| Pacific cod **Gadus macrocephalus** | J-A | 7-60 | U | — | — | — | U | — | — | — | — |
| Pacific herring **Culpea harengus pallasi** | A | 16 | U | — | — | — | U | — | — | — | — |

TABLE 1. Continued.

| Name | Stage of life[1] | Estimated body length (cm) | Before reef was constructed Spring through winter | Seasonal occurrence[2, 3] Near the site of the reef After reef was constructed Spring | Summer | Fall | Winter | On the reef Spring | Summer | Fall | Winter |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Pacific sand lance **Ammodytes hexapterus** | A | 12 | U | U | — | U | — | — | — | — | — |
| Pacific snakeblenny **Lumpenus sagitta** | A | 18 | — | U | — | U | — | — | — | — | — |
| Pacific staghorn sculpin **Leptocottus armatus** | A | 16-27 | U | C | C | C | C | — | — | — | — |
| Padded sculpin **Artedius fenestralis** | A | 6-19 | C | C | C | C | C | C | C | C | C |
| Painted greenling **Oxylebius pictus** | A | 12 | — | — | — | — | — | — | — | U | U |
| Penpoint gunnel **Apodichthys flavidus** | A | 30 | — | — | — | — | U | C | C | C | C |
| Pile perch **Rhacochilus vacca** | J-A | 7-30 | U | U | U | U | U | U | C | C | C |
| Ratfish **Hydrolagus colliei** | A | 60 | U | — | U | C | C | — | — | — | — |
| Red Irish lord **Hemilepidotus hemilepidotus** | A | 34 | U | U | — | — | U | — | — | — | — |
| Rock sole **Lepidopsetta bilineata** | A | 20 | C | C | C | C | C | — | — | — | — |
| Roughback sculpin **Chitonotus pugetensis** | X | 9 | — | N | — | — | N | — | — | — | — |
| Sailfin sculpin **Nautichthys oculofasciatus** | A | 11-15 | U | U | U | U | U | C | C | C | C |
| Salmon **Oncorhynchus** spp. | J | 10 | U | — | — | U | — | — | — | — | — |
| Scalyhead sculpin **Artedius harringtoni** | A | 4-8 | C | C | C | C | C | C | C | C | C |
| Shiner perch **Cymatogaster aggregata** | J-A | 6-11 | C | N | C | C | N | — | C | C | — |

TABLE 1. Continued.

| Name | Stage of life[1] | Estimated body length (cm) | Before reef was constructed Spring through winter | Seasonal occurrence[2, 3] Near the site of the reef After reef was constructed | | | | On the reef | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter |
| Smoothhead sculpin **Artedius lateralis** | A | 6 | C | C | C | C | C | C | C | C | C |
| Spiny dogfish **Squalus acanthias** | A | 70-100 | — | U | — | — | U | — | — | — | — |
| Starry flounder **Platichthys stellatus** | A | 25 | U | U | U | U | U | — | — | — | — |
| Striped seaperch **Embiotoca lateralis** | J-A | 7-30 | C | C | C | C | C | C | C | C | C |
| Sturgeon poacher **Agonus acipenserinus** | X | 12 | — | — | — | — | U | — | — | — | — |
| Tidepool sculpin **Oligocottus maculosus** | X | 5 | U | — | — | — | U | — | — | — | — |
| Tubesnout **Aulorhynchus flavidus** | A | 12 | U | — | C | C | — | — | — | — | — |
| Whitespotted greenling **Hexagrammos stelleri** | A | 20-25 | U | C | — | C | C | — | — | — | — |

[1]A = adult; J = juvenile; X = unknown.

[2]C = common fish; U = uncommon fish; and N = nocturnal fish. Common fish (C) were those species observed on one-half, or more, of the dives and uncommon fish (U) on fewer dives; some species (N) were seen only at night.

[3]Ten dives were made before the reef was constructed; a total of 8 dives were made in the spring, 6 dives in the summer, 17 dives in the fall, and 16 in the winter after the reef was constructed. Two of the winter dives and one of the spring dives were made at night.

ent, especially in the areas of buoyant kelp. Striped seaperch decreased in abundance in the fall; from December to March, relatively few were observed; and from April to May, abundance increased. Abundance of striped seaperch was greatest on or near the reef; in winter, this location was often the only one in which the species was seen.

The shiner perch was estimated to be the next most numerous fish in the study area from June to August. This species used both the reef and adjacent areas. The shiner perch was in the study area during the day in the summer and at night in the winter and spring (night dives were not made in the fall).

Abundance of copper rockfish over the reef and between the reef and adjacent areas varied greatly among seasons (Patten, 1973). The number of copper rockfish counted over the artificial reef was a minimal estimate because many hid in the rocks, especially during the winter. Numbers of copper rockfish were lowest from May to August; their abundance sharply increased and was maximal from September to December. Abundance decreased from December to March and then increased slightly from March to April in some years. Copper rockfish that were solitary or in groups to 10 were infrequently observed through the study area in the bull kelp in August and September. At other times of the year, the reef was usually the only location where they could be found.

The average number of cabezon seen per dive did not change seasonally, but was comparatively greater on the reef. The numbers observed over the study area were 1.4 before the reef was constructed and (exclusive of the reef) 0.8 after. The average number of cabezon observed per dive on the reef was also 0.8. Considering that the extent of the area examined adjacent to the reef was much greater than the area of the reef, cabezon obviously were attracted to the reef.

### Observations on Behavior of Fish

Fish fed, spawned, and sought shelter within the interstices of the reef. Sculpin of the genus *Artedius* and perch were seen feeding on organisms. The reef was used for spawning substrate by a cabezon on 14 June 1964 and by numbers of buffalo sculpin in February and March 1968 and 1969. Large numbers of fish were attracted to the reef apparently for shelter. The copper rockfish, penpoint gunnel (*Apodichthys flavidus*), and small sculpin, common within the interstices of the reef, probably required an environment with protective cover. Such may also have been the case for the sailfin sculpin, which exhibited a negative phototropism and inactivity during the day. Cabezon were too large to pass through the interstices, although they often partially concealed themselves between rocks or under overhanging rocks. Young of the year striped seaperch cruised through or remained stationary within the interstices.

The psychological need the reef provided to the fish is probably a complex study in itself and varies for different species. On this subject, Breder and Nigrelli (1938) described thigmotropism as the 'desire' of fishes to be close to a solid object. The attraction of fishes to each other . . . also becomes a necessary explanation of reef success. Finally, availability of shelter and food helps explain the attractiveness of artificial habitat. (from Carlisle *et al.*, 1964).

The nature of the thigmotropic response of fish to massive objects such as the reef can be analyzed by comparing my impressions of fish abundance over different types of substrate during the day. The lowest density of fish in the study area was over sandy bottoms. Areas with rocky bottoms had a lower density of fish in the tidal zone (when

covered by water) than in the subtidal zone. Large boulders or clusters of noncontiguous boulders were perhaps slightly more attractive to fish than were bottoms made up of smaller rocks. These observations suggest that had the reef been constructed horizontally instead of vertically, had it been placed in the tidal zone, or had it been constructed of large boulders of similar overall dimensions, fewer fish would have used it. Thus, the most important difference between the reef and other types of substrate near the study area was its massiveness and its extensive dark, moderately large interstices. Similarly, Walton's (1979) study of artificial habitats in central Puget Sound showed the greatest density and biomass of fish occurred at the deeper (15 m) structures that had higher relief and more spacious interstices of the configurations used.

Some of my observations confirm the findings of Japanese researchers studying the elements of attraction of fish to physical structures in aquaria. Ogawa and Onoda (1966), Ogawa and Takemura (1966), and Ogawa and Aoyama (1966) reported that only certain species were attracted to physical structures. These authors found that of the fish attracted to physical objects, attraction was greatest when structures were solid rather than open-framed, placed together rather than spread out, and of complicated rather than simple construction. They also noted that larger fish were attracted to larger structures and that buoyant polyethylene tape (artificial seaweed) on structures increased their attraction of fish.


## Summary

A reef of rocks 1.5 m high and 4 m wide constructed in 2.8 m of water was effective in attracting fish. Of the 38 species of fish seen in the study area, 14 [black rockfish (*S. melanops*), brown rockfish, buffalo sculpin, cabezon, copper rockfish, padded sculpin (*Artedius fenestralis*), painted greenling, penpoint gunnel, pile perch, sailfin sculpin, scalyhead sculpin (*A. harringtoni*), shiner perch, smoothhead sculpin (*A. lateralis*), and striped seaperch]—and possibly 3 others (ratfish, spiny dogfish, and white spotted greenling)—used the reef. The cabezon, copper rockfish, striped seaperch, and shiner perch were the most abundant species observed in the study area; all were numerous on the reef. Abundance of fish on the reef and in adjacent types of habitat within the study area was greatest in summer and least in winter. Biomass of fish, however, was always greater on the reef than in the adjacent areas.

Activities of fish associated with the reef included feeding and spawning. Some fish hid within its interstices and on its rough contours. The features of the physical structure of the reef most attractive to the fish were probably its massiveness and its extensive, dark, moderately large interstices.


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# Surficial and Environmental Geology of the Lower Baker Valley, Skagit County, Washington

## Abstract

Many aspects of the late glacial history as well as the types of geologic hazards found in the lower Baker Valley are common to the adjacent parts of the northern Cascade Range. We present a reconnaissance map showing the surficial geology of the lower Baker Valley, Washington, report the discovery of a postglacial pyroclastic flow from Mount Baker and an extensive locally derived mudflow, and discuss environmental hazards posed by mass failures in the glacial deposits. Deposits of the last glaciation (~10,000 to 20,000 YBP) in the region and its geologic history create stratigraphic and topographic settings conducive to slope failures on a variety of scales. Landslides which occurred in early postglacial time are probably related to pervasive fracturing of local bedrock and to slope steepening by glacial erosion. Smaller, recent landslides involving Quaternary material have resulted from natural slope and stratigraphic conditions and the effects of roading and timber harvest practices. Eruptive events on Mount Baker have also affected parts of the Baker Valley throughout postglacial time and include emplacement of a pyroclastic deposit on the floor of lower Baker Valley over 10 km farther downvalley than those previously reported.

## Introduction

The northern Cascade Range of Washington, with its Quaternary volcanic and glacial events, steep slopes, heavy precipitation, and extensive timber harvesting, contains abundant geologic hazards which have been ignored until recently. The lower Baker Valley exemplifies many types of these hazards, including landsliding on a range of scales, stream migration and aggradation, mudflows, and a variety of volcanic hazards in an area of extensive land use for timber harvesting and hydroelectric power generation.

The nature and distribution of surficial deposits in the lower Baker Valley reflect ice-sheet glaciation in mountainous terrain, and postglacial activity on Mount Baker (Hyde and Crandell, 1975; 1978; Frank *et al.*, 1977) whose southeast slopes drain into this area. Heller (1978; 1980) studied deposits of the Fraser Glaciation (~10,000 to 20,000 YBP; Armstrong *et al.*, 1965) in the area, and described large landslides involving surficial material and bedrock. Hyde and Crandell (1978) discussed postglacial tephra, lahars, pyroclastic flows, and lava flows exposed on the east flanks of Mount Baker. They used the stratigraphy of these deposits and $^{14}C$ dating to evaluate the potential hazards associated with continued volcanic activity. Increased thermal activity in Mount Baker's Sherman Crater since early 1975 (Frank *et al.*, 1977) and environmental problems caused by landslides and their downstream effects (Peck, 1967; Heller, 1980,

1981) have sparked interests in the surficial geology of this region. In this paper, we discuss the results of our field studies in the lower Baker Valley, summarize the environmental aspects of previous geologic studies, and present a reconnaissance map showing surficial geology of the area.

### Setting

The lower Baker Valley is located in northwestern Washington (Fig. 1), to the east and southeast of Mount Baker (3287 m), an active stratovolcano near the north end of the Cascade Range. The study area comprises 90 $km^2$, with elevations ranging from 60 to 450 m; topography is generally steep and rugged except for a large area of undissected glacial deposits lying west of Lake Shannon. The climate is mild with warm, dry summers and cool, wet winters. Annual precipitation ranges from 2000 to 3300 mm; most of it falls from October to March; mean annual temperature averages about 10° C in the valleys (Drost and Lombard, 1978).

The heavy timber and thick understory vegetation present in the area is composed of species typical of the western hemlock zone (Franklin and Dyrness, 1973). Rapid revegetation of logged areas makes exposures sparse; therefore, surficial deposits were generally mapped using aerial photographs and exposures of surficial materials and bedrock found along the extensive network of logging roads, in borrow pits, along stream cuts, and in landslide areas. Detailed descriptions of the area and field methods are found in Heller (1978).

### Geology

Mount Baker is a mid- to late-Quaternary stratovolcano built on a base of metasedimentary and metavolcanic rocks (Coombs, 1939). The flanks of the cone are dominated by lahars, alpine drift, and alluvial fans derived from the volcano, and glacial drift deposited by the Puget Lobe of the Cordilleran Ice Sheet (Armstrong *et al.*, 1965). Misch (1966) described the geology and structure of the basement rocks in the lower Baker Valley, and recognized three units, each bounded by thrust faults: (1) the late Paleozoic Chilliwack Group of Daly (1912), consisting of undeformed to mildly metamorphosed sedimentary and igneous rocks; (2) the Shuksan Metamorphic Suite of pre-mid-Cretaceous age (Armstrong, 1980), including actinolite greenschist and crossite and glaucophane schists (Shuksan Greenschist), and pelitic and semipelitic phyllite (Darrington Phyllite); and (3) the Nooksack Group of Mesozoic age, a flysch-like, sedimentary unit locally metamorphosed along fault zones. These regional faults have fractured the bedrock, possibly contributing to the occurrence of large landslides where bedrock is exposed along valley walls.

Surficial deposits in the lower Baker Valley are portrayed in Figure 2. Most of the material was deposited beneath or near the continental ice sheet during the Vashon Stade of the Fraser Glaciation, which lasted from about 17,500 to 13,500 years before present (YBP) in northwestern Washington (Armstrong *et al.*, 1965).

Heller (1978), supplemented by more recent field work, has shown that during the Vashon Stade, continental ice moved eastward up the Skagit Valley, damming the Skagit River and depositing lacustrine and overlying outwash sediments which form a thick fill in the lower Baker Valley and adjacent parts of the Skagit Valley (Fig. 3). The lacustrine silts coarsen upsection and downvalley into well-stratified and cross-

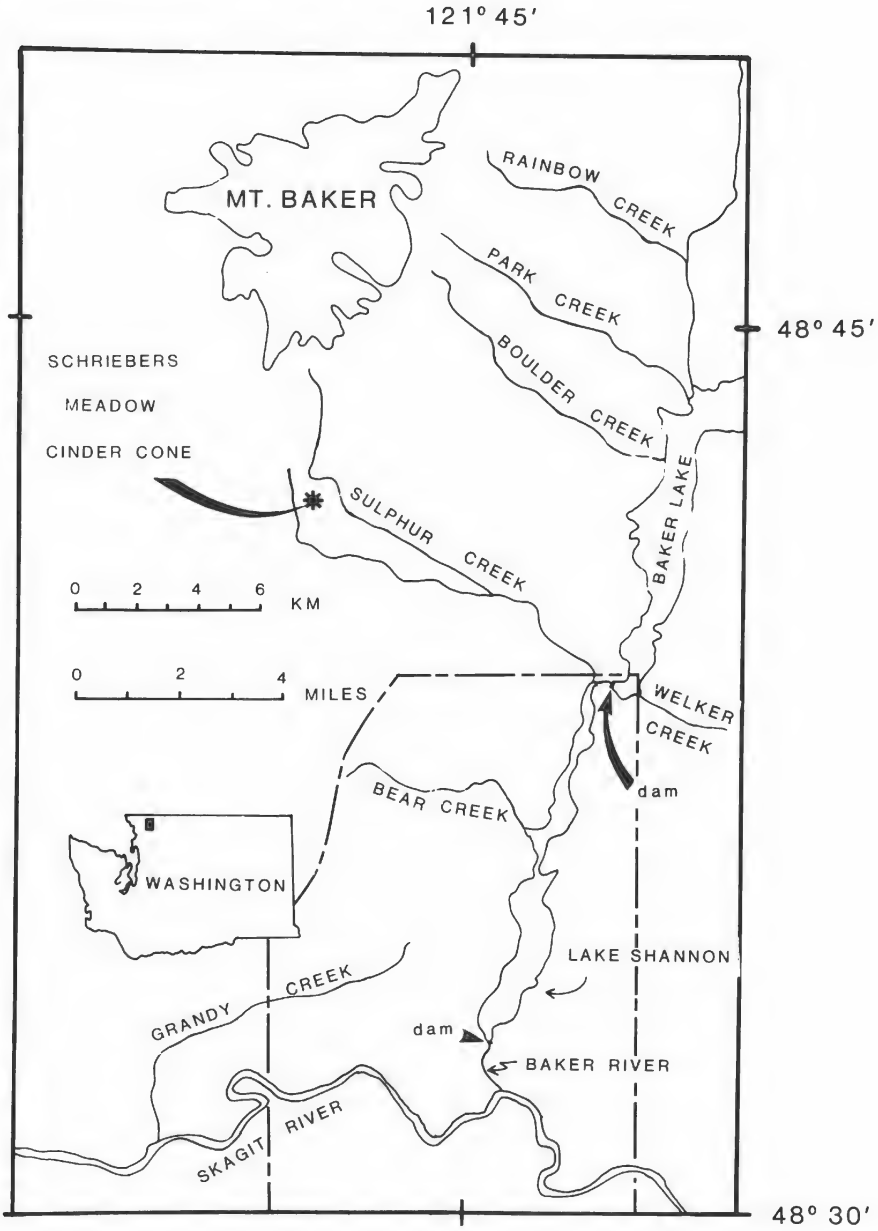


Figure 1. Location map of the lower Baker Valley. Dashed lines show study area boundary.

bedded sand, and sand and gravel. At the culmination of the Vashon glacier advance, ice buried the study area, depositing lodgement till over the lacustrine and outwash sedi-

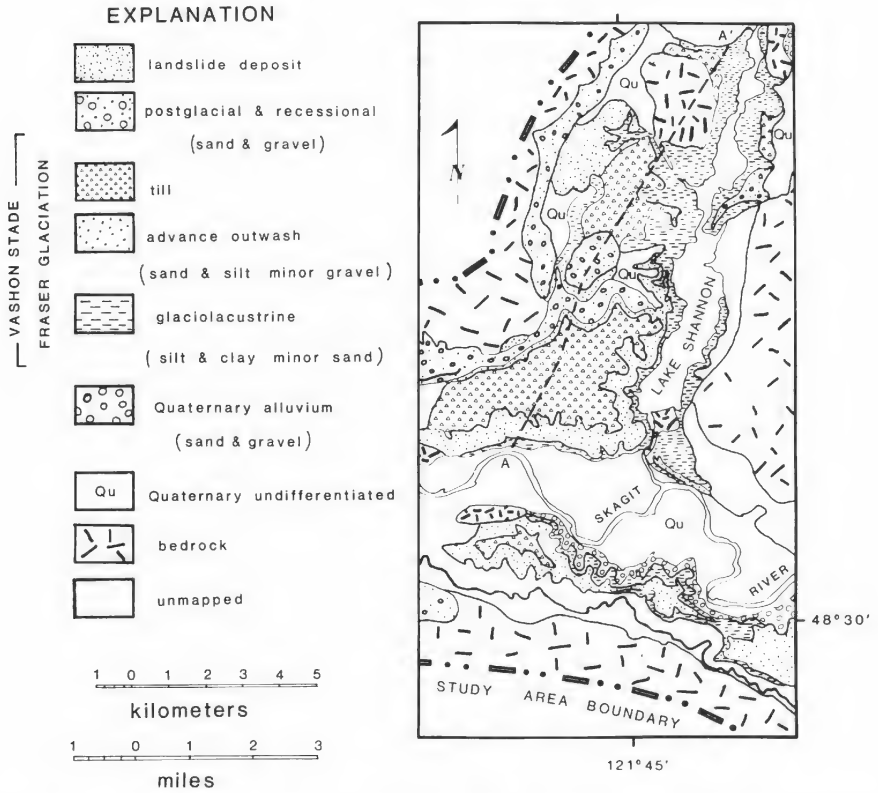


Figure 2. Generalized geologic map of the lower Baker Valley region. Dashed line A-A′ is line of cross section in Figure 3. Modified from Heller (1979c).

ments. Vashon glacier-flow directions, interpreted from stratigraphy and pebble counts in till, suggest that the continental ice advanced up the Skagit and Baker Valleys beyond the limits of the study area. During the glacier maximum, ice flow changed from northward (upvalley) to the south-southeast, across the western Baker Valley divide (Heller, 1979a). During glacier recession, a still-stand of the ice near the Baker Valley mouth resulted in deposition of a large recessional outwash fan (Fig. 3). Several now-abandoned channels including one now occupied by Grandy Creek (Fig. 2) were formed during the final stages of ice recession.

### Early Postglacial Landslides

During deglaciation, it was likely that ponded water, slopes steepened by glacial erosion, sparse vegetation, and earthquakes associated with rapid isostatic rebound (Thorson, 1979) helped cause a large number of landslides in the North Cascades (see Dethier *et al.*, 1980; Whetten *et al.*, 1980). In the Baker Valley, deposits from postglacial slope failures which originated high on the valley walls comprise a large alluvial fan exposed at the mouth of Welker Creek (Fig. 1), just northeast of the head of Lake Shannon (SE1/4 SE1/4, section 31, T37N, R9E). The fan consists of over 60 m of mostly

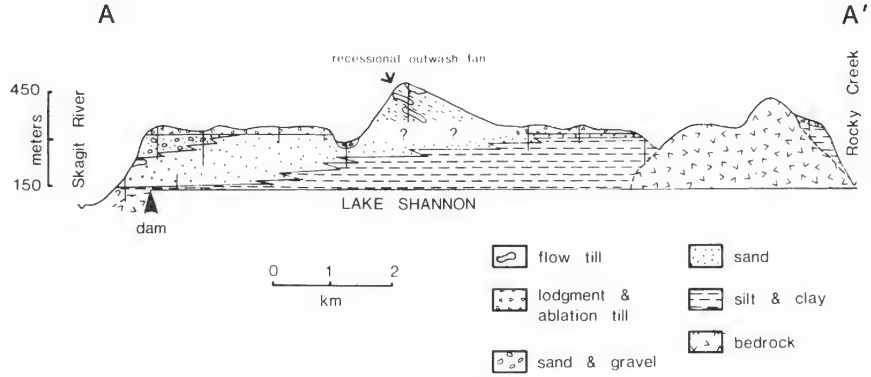


Figure 3. Diagrammatic cross section through the lower Baker Valley. Line of cross section is shown in Figure 2. Vertical lines mark locations of measured and (or) well exposed sections.

Figure 4. View north looking down abandoned outwash channel. Channel is blocked at north end (beyond barn) by small mounds of landslide material.

angular, locally derived, fine sand to boulder (4 m maximum diameter) gravel.

West of Lake Shannon, a partially abandoned, north-sloping outwash channel was dammed by a landslide which emanated from high on the valley walls (Fig. 2). A group of small, rounded hills, representing the most southerly extent of a lobate-shaped hummocky region, blocks the channel at its north end (Fig. 4). These hills and the surrounding area contain abundant angular stones derived from the valley walls.

An exposure along Bear Creek, nearly two kilometers to the northeast of the channel's north end, reveals a mudflow deposit that is probably related to the landslide. There the exposed deposit contains more than 2.7 m of unstratified, poorly sorted,

very angular cobble to boulder gravel with an oxidized fine to coarse sand matrix. Fifty percent of the deposit is gravel-size rock. Exposures along Bear Creek indicate the mudflow becomes finer to the east. A large, cone-shaped depression at the head waters of Bear Creek (Fig. 1) comprises about 4 x $10^7$ $m^3$ and could be the source of the landslide debris. The absolute age of this landslide is unknown. However, the pervasive oxidation of matrix material, subdued topography of the slide surface, and stratigraphic position of the mudflow directly over outwash material suggest that the slide occurred in early postglacial time.

### Landslide Hazards

Slides which involve glacial deposits were initiated in early postglacial time as the Baker River cut through the glacial section near the present location of Lake Shannon. Debris slides, debris flows, and slump flows dominate the landscape around the lake, as well as other steep slopes formed by stream incision. Debris slides are shallow, relatively dry failures, which occur in relatively permeable but noncohesive units such as sand, or sand and gravel, on steep slopes (greater than 50 percent). These failures occur mainly on slopes logged by the clear-cut method. Debris flows, which are spoon-shaped and fail by wet flowage, and slump flows, which have components of rotational and flowage failures, are found on shallower slopes (30-70 percent) in stratigraphic sequences that include a water-perching unit, such as interbedded silts and clays or sands and silts. Slump flows differ from debris flows only in that semi-consolidated material (usually till) is located at the slide heads. Commonly, this impermeable unit is breached during road construction, which may lead to slump flow failure by localizing water infiltration.

A recent compilation of small-landslide activity over the 20-year period ending in 1976 (Heller, 1979b) indicates that 25 percent of the study area (or 23 $km^2$) has unstable or marginally stable slopes (Fig. 5). Of the total number of landslides mapped in the lower Baker Valley (94), 32 percent are debris flows, 27 percent are debris slides, and 21 percent are slump flows, and 10 percent are unclassified. The types of slope failures are largely dependent on the parent material (Fig. 6), slope angle, and timber harvest history (Heller, 1978; 1980). In general, timber-harvest practices, including road construction, have served to aggravate slide problems in this highly-susceptible terrain (Heller, 1980). Swanson and Dyrness (1975) noted similar patterns of sliding in tuffaceous volcanic rocks in the Oregon Cascades. The large contribution of sediment from "natural" and logging-induced slides poses environmental problems for stream and reservoir management in the lower Baker Valley.

As much as 25 percent of the lower Baker Valley area contains unstable to marginally stable slopes, which produce a minimum sediment yield of $6x10^3$ $T/km^2$ yr ($2x10^4$ $t/mi^2$ yr), (Heller, 1980); using this figure, we calculate that the sedimentation rate in Lake Shannon due solely to mass wasting in first- and second-order tributary drainages exceeds 5 mm/yr, or roughly 80 percent of the total sedimentation rate. We have studied slide areas in some detail, but have examined tributary drainages only on a reconnaissance basis. Grandy Creek, and many of its small tributaries, and streams draining into Lake Shannon show evidence of channel disruption (Pfankuch, 1975), including extensive areas of undercut banks, the predominance of fresh gravel in the bed, injury to near channel vegetation, and siltation of extensive areas of gravel. Grandy

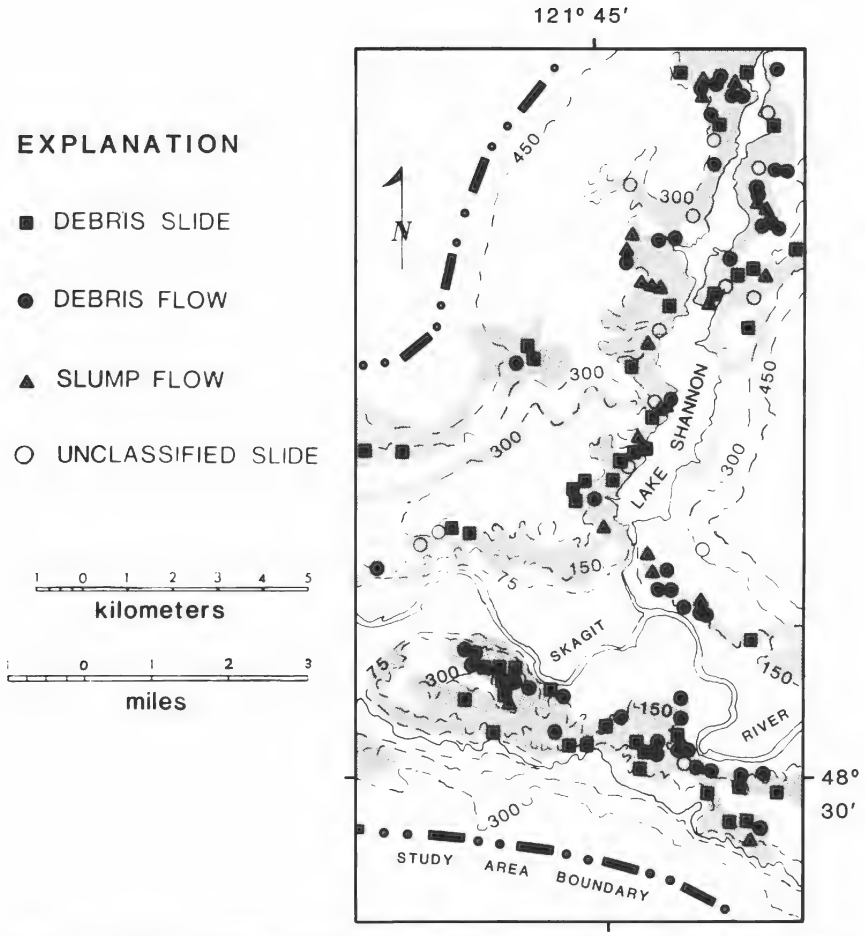


Figure 5. Location of small landslides in Quaternary deposits of the lower Baker Valley. General distribution of unstable and marginally stable areas in these deposits shown with shaded pattern. Unstable slopes developed on bedrock (see Figure 2) not shown. Contours shown are in meters above sea level. Modified from Heller (1979b).

Creek, in particular, has migrated and aggraded rapidly in response to a high sediment influx from slides and roads in clear-cuts. Channel migration and aggradation have repeatedly damaged the adjacent highway and further destabilized the stream banks. Reconnaissance study of aerial photographs suggests that other creeks in the study area have experienced similar, though less spectacular, recent changes. To our knowledge, no quantitative study of channel changes or effects on wildlife have been performed in this area.

Figure 5 shows landslides and highlights areas which have a high landslide potential, based on the slope angle and stratigraphy of glacial deposits (Heller, 1979b). Available evidence does not allow us to separate quantitatively naturally-occurring slides from those which result from timber-harvest activities. However, a comparison of the

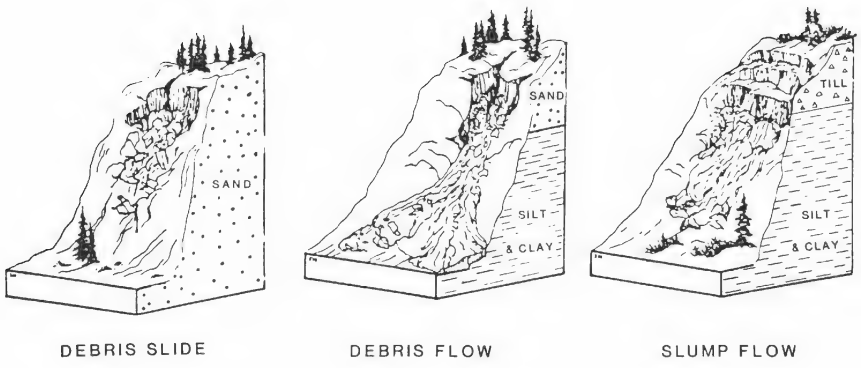


Figure 6. Types of small landslides in study area and their typical stratigraphic situations.

logging history in the area and the distribution of landslides (Heller, 1981) suggests that debris slides are associated with clear-cut logging practices, probably where soils with low cohesion lose strength due to decay of tree roots soon after logging (Swanston, 1974). Though small debris flows (less than 600 $m^2$) are common sights in clear cut areas, there does not appear to be a correlation between logging history and distribution of larger debris flows (Heller, 1980). Slump flows apparently occur where relatively impermeable, semi-consolidated material is breached during road construction, localizing water infiltration (Heller, 1978; 1980). However, the initiating mechanisms for some of the largest landslides in the area—e.g., the ones that destroyed the lower Baker Powerhouse (Peck, 1967)—are still unknown.

### Volcanic Hazards

Hyde and Crandell (1978) noted that major lahars have flowed down Boulder Creek (Fig. 1) about once every 200 years in the late Holocene, and that a pyroclastic flow travelled at least 10 km down the Boulder Creek valley in early Holocene time. The basaltic lava flows which fill Sulphur Creek valley (Sterns and Coombs, 1959; Stavert, 1971) and the cinder deposits in the upper valley were erupted from the Schriebers Meadow cinder cone between 10,400 and 6,900 YBP; the flows and cinders apparently overlie a weathered, postglacial lahar (Hyde and Crandell, 1978). A minimum of seven large mudflows and two lava flows reached portions of lower Baker Valley during postglacial time and tephra from Mount Baker (10,400 and 8700 (?) YBP) and Mount Mazama (6900 YBP) blanketed parts of the valley.

Although Hyde and Crandell (1978) did not find evidence that Holocene pyroclastic flows had travelled beyond the Boulder Creek valley, we have since discovered a pyroclastic flow deposit in an exposure south of the Sulphur Creek drainage. The deposit is exposed in a rock quarry (NE1/4 SW1/4, section 2, T36N, R8E) immediately southwest of a bedrock knob in lower Baker Valley (Fig. 7). The pyroclastic flow is a poorly sorted, unstratified and semi-consolidated deposit consisting of a pebble to boulder gravel with an oxidized fine to coarse sand matrix. Underlying this deposit is less than two meters of compact, unoxidized, stoney till of Vashon age which mantles metasedimentary bedrock. The pyroclastic flow is about two meters thick, and con-

Figure 7. Rock quarry in lower Baker Valley exposing pyroclastic flow (PF), underlying till of Vashon age (TL) and bedrock (BX). Mount Baker in distance.

sists of 30 to 40 percent subrounded to subangular gravel-size material; 97 percent of the clasts are porphyritic andesite of Mount Baker origin, and more than half of them are vesicular. Initially, we believed that the deposit was a lahar. However, study of the remnant magnetism of oriented clasts (see Appendix) showed that most of them display uniform and parallel thermoremnant magnetism (TRM), suggesting that they cooled through their Curie temperature after coming to rest (Aramaki and Akimoto, 1957). Using the criteria suggested by Hoblitt and Kellogg (1979), we determined that the volcanic diamicton is probably a pyroclastic flow deposit.

The extent of the pyroclastic flow is unknown. D. Frank (pers. comm., 1980) reports that a weathered, volcanic-rich diamicton overlies bedrock in a roadcut about one kilometer north of the rock quarry. The weathered, pre-cinder cone lahar reported (Hyde and Crandell, 1978) in the upper Sulphur Creek valley might instead be a pyroclastic flow, as might some of the diamictons, interpreted as till, which were found in well borings near the mouth of Sulphur Creek (Sterns and Coombs, 1958; 1959). Because the till at the quarry is apparently unweathered and was deposited during the Vashon Stade, the overlying weathered pyroclastic flow is of latest Pleistocene or early Holocene age. The origin of the pyroclastic flow exposed at the quarry is unknown. The abundance of vesicular rocks and the location of the deposit suggest that the flow travelled down the Sulphur Creek valley. However, the only documented postglacial pyroclastic flows occur in the Boulder Creek area, and the stratigraphy of deposits underlying the exposed lavas of Sulphur Creek is not well known. Regardless of where the

flow originated, it is exposed at least 10 km farther downvalley than previously known flows, and probably reached the present site of the Upper Baker Dam. Detailed field study will be required to place more accurately the pyroclastic flow in the stratigraphy of the Mount Baker area. The newly recognized pyroclastic flow suggests that the zone of hazard from pyroclastic-flow activity (cf. Hyde and Crandell, 1978) should extend to portions of the lower Baker Valley, perhaps as far as Lake Shannon, pending more detailed mapping in the area.


#### Summary

Stratigraphic relationships in the glacial deposits, steep slopes, and logging activity contribute to a pattern of frequent mass movement, disrupted stream channels, and rapid sedimentation of lakes and reservoirs in the lower Baker Valley. Lahars from Mount Baker have reached the lower Baker Valley near the mouth of Boulder Creek, and new evidence shows that at least one pyroclastic flow has reached the area since the Fraser Glaciation. Future work in this area should examine the areal distribution of the pyroclastic flow, and study the causes of slope failure in more detail.



#### Acknowledgments

The authors would like to thank Myrl E. Beck and Jack H. Hyde for their field guidance and discussions, and John Spasari for his field and laboratory assistance. Support was provided by the Skagit County Planning Department and the Washington State Department of Natural Resources.


#### Appendix

*Pyroclastic flow sampling and identification*: ten oriented stones of subspherical shape, ranging from fist-sized cobbles to small boulders were collected at the rock quarry. These were examined in the laboratory at Western Washington University with a Vickers Magnetometer Model PM-1. Eight stones revealed remnant magnetic directions paralleling each other and today's magnetic field within the measuring accuracy of the method (approximately $\pm$ 5°). Two stones were found to be 180° out of phase and are thought to have been incorrectly marked in the field.

To test the possibility that secondary magnetism acquired at low temperatures had realigned an initially random set of directions of remnant magnetism along the present field (i.e., viscous remnant magnetism), an unoriented specimen from a representative boulder was demagnetized in an alternating magnetic field of up to 500 oe intensity. The specimen showed extreme directional stability and had a median destructive field of more than 400 oe. This finding makes it seem extremely unlikely that the deposit could have acquired much low temperature, secondary magnetism (M. E. Beck, Jr., pers. comm., 1978).

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## Association News

The 54th Annual Meeting of the Northwest Scientific Association was held at Oregon State University on March 26-28. Highlights of the meeting included two invited symposia entitled "Forest Succession in the Northwest" and "Mt. St. Helens." The Association also enjoyed the banquet speech by Dr. Charles Rosenfeld, "Remote Sensing of the Volcanic Eruptions of Mt. St. Helens, WA;" and a paper session cosponsored by the Botany, Forestry, and Zoology Sections, "Evolutionary Biology."

Dr. Richard B. Walker, Professor of Botany at the University of Washington, received the Outstanding Scientist Award given by the Association in recognition of his scientific contributions in the plant sciences. Research grant awards were given to Cherri C. Van Doren, Department of Biology, Walla Walla College; Christopher Topik, Department of Biology, University of Oregon; and Nalini M. Nadkarni, College of Forest Resources, University of Washington.

The new officers of the Association are: President, James R. Chambers; Vice President, John H. Perkins; Secretary, Robert Carson; and Treasurer, Robert J. Jonas. Five new Trustees were elected to the Board. They are Denis P. Lavender, Donald Minore, Richard J. Naskali, Ronald H. Sauer, and Robert Zasoski.

The Trustees and Members approved an increase of individual and institutional memberships for 1982. Regular memberships will be $14 and student memberships will be $8. A $1 discount will be given for memberships paid before January 15.

William R. Rayburn, Secretary

The following reprint and page charges for Northwest Science will be effective for all papers printed after 1 January 1982:

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Page charges will increase to $50 per page.

# EFFECT OF ST. HELENS ERUPTION ON THE TIMBER RESOURCE, GIFFORD PINCHOT NATIONAL FOREST

## SUMMARY

Table 3

**National Forest Land Acre Summary***
**Lands Damaged by the Mount St. Helens Eruption**

| Pre-Eruption Timber Stands | Post Eruption Condition | | | | |
|---|---|---|---|---|---|
| | Total Acres | Barren | Down | Damaged | Water |
| Large Sawlogs | 24,470 | 3,960 | 15,690 | 4,020 | 800 |
| Small Sawlogs | 9,520 | 5,590 | 3,550 | 280 | 100 |
| Poles | 1,850 | 270 | 860 | 710 | |
| Saplings | 4,330 | 2,560 | 1,680 | 90 | |
| Seedlings | 770 | 420 | 170 | 190 | |
| Nonstocked | 450 | 450 | | | |
| Noncommercial Lands | 19,850 | 17,820 | 1,260 | 760 | 10 |
| Total 41% | 61,240 | 31,070 | 23,210 | 6,050 | 910 |

*Based on 6/19/80 U-2 photo interpretation and subsequent adjustment into known pre-eruption data base. Current as of 10/7/80.

Table 4

**State and Private Land Acre Summary**
**Lands Damaged by the Mount St. Helens Eruption**

| Pre-Eruption Timber Stands | Post Eruption Condition | | | | |
|---|---|---|---|---|---|
| | Total Acres | Barren | Down | Damaged | Water |
| State | | | | | |
| Merchantable | 3,750 | 400 | 2,560 | 780 | 10 |
| Non-merchantable | 8,510 | 2,230 | 4,280 | 1,910 | 90 |
| Total 8% | 12,260 | 2,630 | 6,840 | 2,690 | 100 |
| Private | | | | | |
| Merchantable | 43,020 | 8,880 | 20,230 | 13,720 | 190 |
| Non-merchantable | 34,110 | 31,090 | 1,510 | 1,210 | 300 |
| Total 51% | 77,130 | 39,970 | 21,740 | 14,930 | 490 |
| Totals | | | | | |
| Merchantable | 46,770 | 9,280 | 22,790 | 14,500 | 200 |
| Non-Merchantable | 42,620 | 33,320 | 5,790 | 3,120 | 390 |
| Grand Total | 89,390 | 42,600 | 28,580 | 17,620 | 590 |

National Forest timber inventory lost is 500 million net board feet, equivalent to a home for every person living in Vancouver, Washington. Value loss is about $125 million. Of the $400 million value affected, about $190 million is recoverable. $2 million loss to young stands.

Recovery

Stable forests in 200 years but will be delayed by further eruptive activity. Viable root stocks and snowpack areas will serve as centers for natural recovery of vegetation.

Erosion seeding on 8250 acres of National Forest land and 11500 acres of other ownerships. Only small areas are effectively reducing erosion.

Reforestation tests to be conducted on a variety of conditions this year (1981). Large scale activities to be initiated in 1982.

Research and Information Needs

1) Vegetative response in ash, especially tree species.
2) Long-term effects and growth trends in ash covered forests.

If you can provide any written information regarding the above, please send to:

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# A Pleistocene Low-Elevation Subalpine Forest in the Western Cascades, Oregon

## Abstract

A boulder diamicton exposed in the low Lookout Creek valley, western Cascades, Oregon, contains fossil wood, needle, and pollen material representative of a Pleistocene flora > 35,500 radiocarbon years in age. The deposit was probably formed by a debris torrent from a tributary watershed. Some of the wood fragments are abraded and randomly oriented, suggesting transport from upslope areas. *Abies* sp., *Pseudotsuga menziesii*, and *Thuja plicata* are represented in these wood specimens. Other materials, including unabraded wood, needles, and pollen occur in a continuous, horizontal layer that may represent a small piece of locally formed forest floor litter. This valley bottom flora contained abundant *Picea* cf. *englemannii* and *Abies* cf. *lasiocarpa*. These fossils suggest the occurrence of *Picea englemannii/Abies lasiocarpa* forest in a cold valley bottom with more xeric forest communities on adjacent hillslopes.

Present arboreal vegetation at the site is dominated by *Tsuga heterophylla, Thuja plicata*, and *Pseudotsuga menziesii*. Modern examples of the community represented by the fossil assemblage occur at elevations over 1000 m higher than the Lookout Creek site. The Lookout Creek assemblage probably represents a flora of an early Wisconsin or previous glaciation under conditions significantly drier than those prevailing during late Wisconsin glaciation.

## Introduction

Preservation of Pleistocene plant fossil material of pre-late Wisconsin age is rather rare, particularly in the steep, rapidly eroding mountainous terrain of the Pacific Northwest. Previous work on materials of this age in western Washington has centered in the Puget Lowland (Hansen, 1938; Hansen and Mackin, 1940, 1949; Easterbrook *et al.*, 1967; Hansen and Easterbrook 1974) and along the coast of the Olympic Peninsula (Heusser, 1964, 1972; Florer, 1972) in areas where the stratigraphy is well known. There have been no reports of known pre-late Wisconsin Pleistocene assemblages in western Oregon, although several undated samples (Hansen and Allison, 1942; Hansen, 1947) may represent this period. We use the term late-Wisconsin to indicate the

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time period between approximately 10,000 and 35,000 years before present (B.P.) when extensive glaciation was occurring in the Northwest, as indicated by the Evans Creek (Crandell and Miller, 1974), Cabot Creek (Scott, 1977), and other drifts. The term early-Wisconsin is used to indicate earlier Wisconsin time, which may be represented in part by Hayden Creek (Crandell and Miller, 1974), Jack Creek (Scott, 1977), and other drifts.

During geomorphic studies in the vicinity of Lookout Creek, H. J. Andrews Experimental Forest, western Cascades, Oregon, we have located an assemblage of wood fragments, conifer needles, and pollen more than 35,000 radiocarbon years in age. In this report we offer an analysis of this assemblage and its implications regarding the magnitude of vegetation displacement in response to major episodes of climatic change. Species identification of the plant material is aided by the presence of both macro- and microfossils.

#### Location, Nature, and Age of the Deposit

The Lookout Creek assemblage is exposed in a streambank at an elevation of 425 m along Lookout Creek, about 1.2 km upstream from its confluence with Blue River (NW ¼ SE ¼ Sec. 31 T15S R5E). The site is within the H. J. Andrews Experimental Forest approximately 55 km east of Eugene, Oregon (Fig. 1). The general geologic and geomorphic settings of the site have been described by Swanson and James (1975a, b).

Plant fossil material is contained within the dense clayey matrix of a bouldery diamicton up to 4.5 m in thickness which is overlain by varved lacustrine sediments (Fig. 1). The lake sediments were presumably deposited in the lower Blue River drainage while the mouth of the river was dammed by glacial ice in the McKenzie River valley (Swanson and James, 1975b). Coarse well-rounded gravel deposited by Lookout Creek rests on both the lacustrine sediments and the diamicton.

The diamicton is exposed at the distal end of a massive debris fan constructed at the mouth of experimental Watershed 2 (Swanson and James, 1975b). Fans constructed of debris torrent deposits occur commonly at the mouths of 5 to 100 ha watersheds in the study area (Swanson and James, 1975b).

Clasts within the diamicton are subangular and up to 80 cm in diameter. No evidence of striations or faceting was observed. The matrix material is a dense compact of blue-gray clay and angular to subangular, unsorted rock fragments. The proportion of rock types in the deposit indicates a source area in nearby watersheds tributary to Lookout Creek, probably Watershed 2. Modern gravel in Lookout Creek includes a variety of rock types not observed in Watershed 2 or in the fossil bearing deposit.

The probable origin of the deposit was a debris torrent which originated at a middle to upper elevation site (600 to 900 m) in Watershed 2. Glaciation would be an alternative means of forming such a deposit. However, the lack of glacial landforms and striations and facets on stones argues against glacial processes as the mode of origin of the deposit. There is no clear evidence of the presence of glaciers along this section of valley floor anywhere within a kilometer of the site.

The fossil material occurs in two different patterns within the diamicton. At locality LOK-1 (Fig. 1), a matted, irregular but continuous layer of twigs, needles, and wood fragments up to several centimeters in thickness extends for more than 4 m

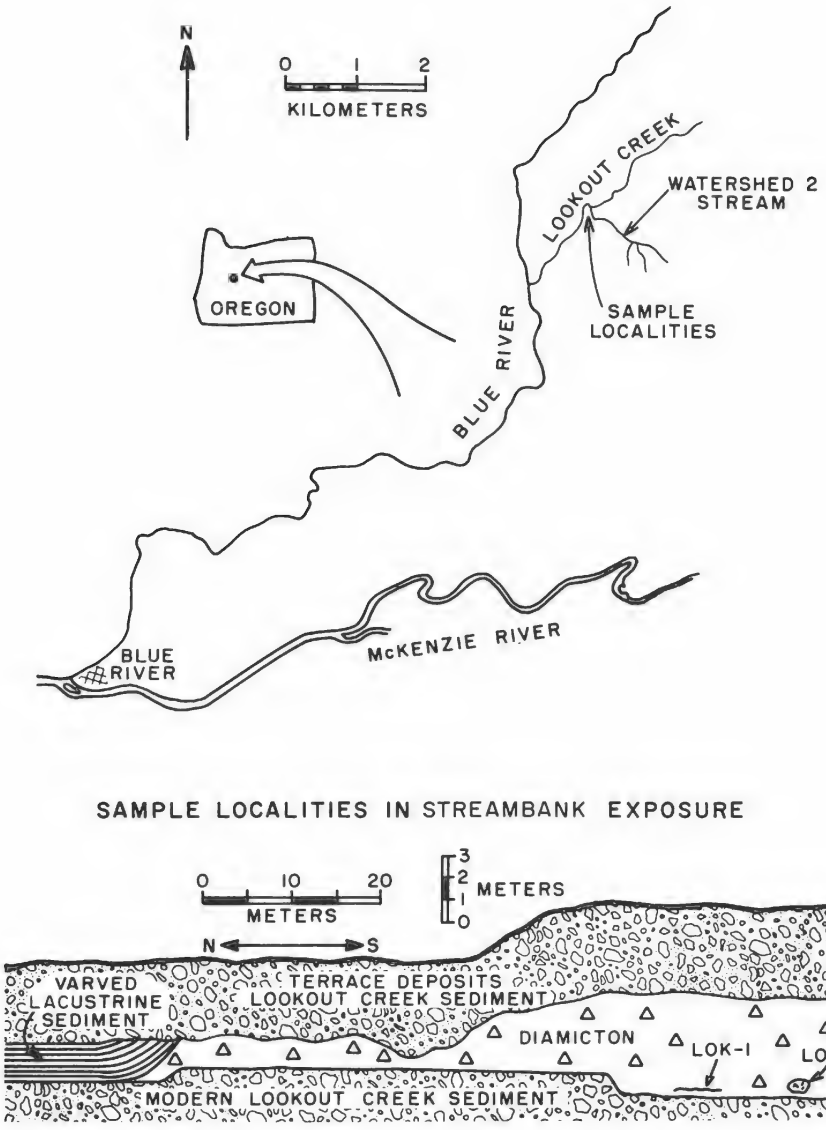


Figure 1. Location of sample localities and sketch of Lookout Creek streambank exposure showing LOK-1 and LOK-2 sites. The modern Lookout Creek sediment is deposited against the base of the exposure which shows terrace deposits unconformably overlying varved lacustrine and diamicton deposits.

horizontally. This fossil bearing horizon does not occupy a noticeable break in lithology or a weathered zone. However, the thin, continuous, horizontal nature of the band, the occurrence of needles arranged along twigs as they were in life, and lack of abra-

sion and rounding of the wood fragments suggest that the deposit represents a piece of intact forest floor which was not subjected to transport in a mass movement event.

Locality LOK-2 (Fig. 1) yields isolated pieces of wood scattered through a zone about 1 m thick within the diamicton. These wood fragments are randomly oriented and rounded and abraded, indicating possible transport in a mass movement event from an upslope area.

Based on these observations and geomorphic studies in Watershed 2 (D. N. Swanston and F. J. Swanson, unpubl. map), we hypothesize that the following sequence of events led to preservation of plant materials at LOK-1 and LOK-2. A debris torrent originated in Watershed 2 at an elevation between 600 and 900 m. In its downstream movement the torrent entrained, transported, and then deposited wood at LOK-2. The wood, twigs, needles, and pollen in LOK-1 appear to have been directly deposited by litterfall onto fresh debris torrent material and soon thereafter covered with similar material. Small scale slumping of debris torrent material, perhaps at a bank eroded by high stream flow, may have covered and preserved the LOK-1 material.

A sample of wood from the diamicton (I-7287) was $C^{14}$ dated at $>$ 35,500 years [B.P.]. The exact stratigraphic position of this specimen relative to the two sample localities is uncertain, but it probably derives from LOK-2. The presence of these deposits at the base of a deeply incised, rapidly eroding watershed suggests that they are not older than Pleistocene and are probably of late Pleistocene age.

#### Analysis of Macrofossils

On 3 June 1976 wood samples, needles, and bulk maceration samples were collected from locality LOK-1, and on 3 June and 7 December 1976 wood samples were collected from locality LOK-2. Ten wood samples from LOK-1 have been determined as *Abies* sp. by Allan Doerksen (Forest Research Lab, Oregon State Univ., Corvallis). The specimens include large diameter stems as well as branches as small as 1 cm. Examination of the leaf material discloses matted needles draped over numerous small twigs. Many of the needles are arranged in parallel clusters or along small twigs. Preservation of the needles is excellent and three dimensional. Disaggregation of the matrix with detergent solution allows intact needles to be separated from the matrix. Bulk maceration of several kilograms of material has not yielded any plant material not referable to *Abies*.

The needles are stomatiferous above and below, shallowly depressed to mildly convex above, flattened, with revolute margins and blunt apices, some of which are minutely notched. The needles are commonly falcate and short, and most are bent at the petiole. The twigs have conspicuous leaf scars. Comparison of these needles and twigs with all species of northwestern *Abies* shows they are clearly referable to *Abies lasiocarpa*. Examination of additional material from LOK-1 by Art McKee (School of Forestry, Oregon State Univ.) disclosed small amounts of *Tsuga heterophylla* and *Picea* sp. (cf. *englemannii*) needles in addition to abundant *Abies lasiocarpa* material.

The wood specimens from LOK-2 appear abraded and rounded. Specimens are referable to *Thuja plicata* (4 specimens), *Pseudotsuga menziesii* (2 specimens), and *Abies* sp. (1 specimen). The *Pseudotsuga* specimens are fragments of large diameter stems and are unusual in their minute growth increments, 0.14 and 0.10 mm/year

(0.005 and 0.004 inch/year). The $C^{14}$ date of > 35,500 B.P. reported above is based on a specimen determined as *Tsuga heterophylla* (or *Libocedrus decurrens*).

#### Analysis of Microfossils

Abundant but generally compressed and poorly preserved pollen and spores have been recovered from locality LOK-1. A pollen count of 250 grains is given in Table 1. Percentages are calculated excluding indeterminate grains, which are those too poorly preserved for positive identification. Shown in Table 2 is a pollen count of 500 grains from a modern stand several hundred meters upslope from the Lookout Creek locality. The modern pollen rain was sampled by collection of 1 cc fragments of five moss polsters within the 50 m x 50 m of Reference Stand 7 (Dyrness *et al.*, 1974; Zobel *et al.*, 1976). These polsters were collected on logs of decay class 4, which have a mean residence time on the forest floor of 82 years (P. C. MacMillan, pers. comm., 1977).

In the pollen counts, *Pinus* species have been provisionally separated using a technique similar to Hansen and Cushing (1973). The basic separation is by cappula ornamentation. Among the diploxylon pines (types with smooth cappulae), the separation of *Pinus ponderosa* from *Pinus contorta* by morphology and size is believed to be reasonably reliable. The separation of haploxylon pines (rough cappulae) *Pinus*

TABLE 1. Pollen analysis of sample from LOK-1. Percentage figures calculated on basic sum, excluding indeterminate grains. Total count = 250 grains. Basic sum = 195.

| | |
|---|---|
| **Abies lasiocarpa** type | 10.8% |
| **Abies procera-amabilis** type | 3.1% |
| **Abies concolor-grandis** type | 2.6% |
| **Abies** indet. | 5.1% |
| Total **Abies** | 21.5% |
| **Picea** | 7.7% |
| **Pinus** diplox. (**contorta** type) | 6.1% |
| **Pinus** haplox. (**monticola** type) | 3.6% |
| **Pinus** haplox. (**albicaulis** type) | 5.6% |
| **Pinus** indet. | 8.2% |
| Total **Pinus** | 23.6% |
| Cupressaceae | 5.1% |
| **Tsuga heterophylla** | 2.1% |
| **Tsuga mertensiana** | 2.1% |
| **Quercus?** | 5.6% |
| TOTAL ARBOREAL POLLEN | 67.7% |
| **Artemesia** | 4.6% |
| **Ribes** | 0.5% |
| **Alnus** | 0.5% |
| **Acer circinatum** | 0.5% |
| Compositae, hi spine | 6.1% |
| Compositae, low spine | 6.1% |
| Cruciferae | 3.6% |
| Cruciferae, cf. **Erysimum** | 0.5% |
| Umbelliferae | 1.5% |
| Saxifragaceae? | 1.0% |
| Rosaceae | 0.5% |
| Malvaceae? | 1.5% |
| Cyperaceae | 0.5% |
| Other herbs | 3.0% |
| Unknown | 2.1% |
| Total shrubs | 6.1% |
| Total herbs | 24.1% |
| TOTAL NON-ARBOREAL POLLEN | 30.2% |

TABLE 2. Pollen analysis and stand data for Reference Stand 7, H. J. Andrews Experimental Forest (Zobel et al., 1974). Pollen analysis based on count of 500 grains. Stand data are in percent cover for mature (M) and reproduction (R) tree species (G. M. Hawk, pers. comm.).

| | | |
|---|---|---|
| **Pollen Analysis-Reference Stand 7** | | |
| **Tsuga heterophylla** | | 35.4% |
| **Pseudotsuga menziesii** | | 24.2% |
| **Abies** spp. | | 0.2% |
| **Pinus** diplox. (**contorta** type) | | 1.4% |
| **Pinus** haplox. (**monticola** type) | | 2.4% |
| **Pinus** indet. | | 0.8% |
| Total **Pinus** | | 4.6% |
| Cupressaceae | | 5.6% |
| **Taxus** | | 1.2% |
| **Alnus** | | 2.8% |
| **Acer circinatum** | | 0.4% |
| **Acer macrophyllum** | | 0.2% |
| **Ceanothus** | | 0.2% |
| TOTAL ARBOREAL POLLEN | | 70.0% |
| TOTAL SHRUBS | | 5.0% |
| **Polystichum munitum** | | 15.8% |
| **Polypodium glycyrrhiza** | | 0.2% |
| **Athyrium?** | | 0.2% |
| Other fern | | 5.0% |
| Liliaceae | | 1.2% |
| Malvaceae | | 0.2% |
| Graminae | | 0.2% |
| Compositae | | 0.8% |
| Cheno-Am | | 0.2% |
| Unknown | | 1.2% |
| Indet. | | 0.6% |
| TOTAL NON-ARBOREAL POLLEN | | 26.6% |
| **Stand Data-Reference Stand 7** | | |
| **Tsuga heterophylla** | M | 55.0% |
| | R | 30.0% |
| **Pseudotsuga menziesii** | M | 25.0% |
| **Thuja plicata** | M | 30.0% |
| | R | 10.0% |
| Total Tree Cover | | 150.0% |
| **Acer circinatum** | | 8.3% |
| **Cornus nuttallii** | | 2.9% |
| **Vaccinium parvifolium** | | 1.8% |
| **Taxus brevifolia** | | 1.3% |
| Total Shrub Cover | | 14.3% |
| **Gaultheria shallon** | | 1.5% |
| **Rubus ursinus** | | 1.3% |
| **Berberis nervosa** | | 0.5% |
| **Rubus nivalis** | | present |
| Total Low Shrub Cover | | 3.3% |
| **Oxalis oregana** | | 24.4% |
| **Polystichum munitum** | | 6.7% |
| **Linnea borealis** | | 5.1% |
| **Coptis laciniata** | | 2.0% |
| **Tiarella unifoliata** | | 2.0% |
| **Viola sempervirens** | | 0.6% |
| **Goodyera oblongifolia** | | 0.1% |
| **Vancouveria hexandra** | | 0.1% |
| **Galium triflorum** | | 0.1% |
| Total Herb Cover | | 41.1% |

*albicaulis, P. monticola,* and *P. lambertiana* is more difficult, but with care seems practical. Although the reported percentages may be open to some question, both *Pinus monticola* and *P. albicaulis* are represented in the LOK-1 pollen sample. A grain referable to *Pinus lambertiana* was observed scanning the modern comparative material from Reference Stand 7 near the Lookout Creek locality.

*Abies* species determinations are more perplexing than those of *Pinus* largely because of the apparent great variability of pollen morphology among species of *Abies* and the difficulty of securing adequate comparative material. Most distinctive of the six northwest *Abies* species is *Abies lasiocarpa.* It is characterized by a relatively thin cappa with fine infrastructure and conspicuous proximal thinning, finely reticulate sacci, and relatively small overall size (Hansen, 1947; Heusser, 1964). *Abies amabilis* and *A. procera* are also distinguishable by their greatly thickened cappae and characteristically thick and dense saccus infraornamentation.

Pollen tentatively determined as *Quercus* (Table 1) resembles the pollen of modern *Q. saddleriana* and *Q. vaccinifolia,* but is considerably larger, generally 45-55 $\mu$, and may represent some other taxon.

Pollen of Cupressaceae in Reference Stand 7 is likely from *Thuja plicata.* Cupressaceae in LOK-1 may be from *Chamaecyparis nootkatensis, Thuja plicata, Juniperus communis,* or perhaps *J. occidentalis.* More probably one or several of the first three species are represented.

Reference Stand 7 typifies the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* (TSHE/POMU-OXOR) community of Dyrness *et al.* (1974) and may be taken as representative of the modern vegetation of the Lookout Creek locality. Species composition data for the stand (Table 2) are available for comparison with the pollen count. Observations of Zobel *et al.* (1976) indicate that this community occupies the warm moist extreme of environments in the central western Cascades of Oregon as shown by indirect (Dyrness *et al.,* 1974) and direct (Zobel *et al.,* 1976) gradient analysis.

#### Interpretation and Discussion

The fossil assemblage from the diamicton at Lookout Creek stands in sharp contrast to the present vegetation. Today the site is at the warm moist extreme of the spectrum of forest community environments in the central Oregon Cascades. The modern pollen rain reflects the present vegetation composition fairly well (Table 2). The rank order of dominant trees, *Tsuga heterophylla, Pseudotsuga menziesii, Thuja plicata,* is repeated in the pollen frequencies. Among the shrubs, *Acer circinatum* and *Taxus brevifolia* are found in the pollen sample. *Alnus rubra* grows in an area near Reference Stand 7. The importance of *Polystichum* is duplicated in the pollen assemblage; however, other herbaceous species are not present at detectable levels. Present at low levels in Reference Stand 7 are *Trillium ovatum, Disporum hookeri,* and *Smilacina stellata,* probable sources of the Liliaceae pollen type, and *Bromus* sp., a possible source of the Graminae pollen.

The LOK-1 pollen assemblage is characterized by a low pine component (24 percent), compared to other glacial period records, high *Abies* (22 percent), moderate *Picea* (8 percent), low *Tsuga* spp., and no *Pseudotsuga.* Comparable Pleistocene pollen assemblages are not common. Only the basal layers of the Scotts Mills and Lake

Kachess cores reported by Hansen (1947) approach that of the Lookout Creek assemblage. The Lake Kachess core from the Central Washington Cascades has much higher *Picea* and *Abies*, about 40 percent pine, and some *Pseudotsuga* and both species of *Tsuga* in low abundance. The basal levels of the Scotts Mills core also contain higher pine and high *Abies* (40-60 percent) and *Tsuga mertensiana* is apparently absent. These cores were studied before the advent of radiocarbon dating and the precise chronological position of their lowermost levels can only be inferential. Here they are interpreted as late Glacial.

The absence of *Pseudotsuga* pollen in the LOK-1 sample is noteworthy. It is generally believed that *Pseudotsuga* pollen is greatly underrepresented in pollen assemblages. However, the sample from Reference Stand 7 indicates that in at least some stands in the Cascades, *Pseudotsuga* pollen is represented in proportion to its coverage. The high settling velocities of *Pseudotsuga* pollen result in impact of virtually all of the pollen within a few hundred meters of the source tree. However, its complete absence in the LOK-1 sample probably indicates that it was not important or vigorous in the area at that time interval. The climate on surrounding upland slopes may have been too extreme for abundant pollen production by *Pseudotsuga.* The extremely low growth rate of the *Pseudotsuga* specimens favors this interpretation. Furthermore, there is some evidence from modern stands to suggest that *Pseudotsuga menziesii* is proportionally underrepresented in the pollen rain in higher elevation stands as compared with low elevation stands (A. S. Gottesfeld and L. M. J. Gottesfeld, unpubl. data).

The fossil assemblage contains macrofossil material of subalpine fir, and the pollen assemblage, containing 8 percent *Picea,* suggests that stands including *Picea englemannii* were nearby. Jonassen (1950) reports that the proportion of *Picea excelsa* pollen in Denmark drops from 59 percent to 7 percent within 200 m of the edge of a spruce forest. *Picea englemannii* wood has been collected 1.8 km south of the LOK locality in glacio-fluvial deposits probably correlative to the varved sediments which overlie the LOK diamicton. The *Picea* wood occurs with wood of *Taxus brevifolia* and *Pinus* cf. *contorta. Picea englemannii* wood has also been recovered from a diamicton similar to the LOK sediments 1 km north of the sample locality. The LOK-1 pollen assemblage contains other indicators of subalpine conditions; e.g., *Pinus contorta, P. albicaulis, Tsuga mertensiana*, and high levels of non-fern herbaceous pollen (21 percent in LOK-1 vs. 2 percent in Reference Stand 7).

Today *Picea englemannii* is generally rare in subalpine communities of the western Cascades, being more characteristic of the eastern slopes of the Cascades and interior ranges. Franklin and Mitchell (1967) find *Picea englemannii* as an important associate of *Abies lasiocarpa* only on the eastern slope of the Washington Cascades, where the forests are transitional to the spruce-fir subalpine forests of the Rocky Mountains. In this area, *Tsuga mertensiana* is generally only a minor associate of *Abies lasiocarpa*, a situation similar to that shown in the LOK-1 pollen assemblage. On the east side of the Cascade Range, especially in Washington, *Abies lasiocarpa* and *Picea englemannii* are also important constituents of forests of deep glaciated valley floors and frost pockets, particularly at elevations above 800 m (Franklin and Mitchell, 1967; Franklin and Dyrness, 1973; Daubenmire and Daubenmire, 1968). In such sites, well developed *Abies lasiocarpa-Picea englemannii* stands may exist below slopes supporting trees of higher temperature requirements (topographic reversal of vegetation zonation).

This finding may be analogous to the situation at LOK-1 where the LOK-2 wood specimens indicate proximity of trees with higher thermal requirements.

The occurrence of pollen of *Picea englemannii* in the western Cascades as well as pollen of *Quercus?*, *Artemsia*, and Compositae at levels much higher than at present suggests a relatively dry as well as cold climate during this glacial event. Pollen records of the Willamette lowland such as those of Lake Labish, Onion Flats, Fargher Lake (Hansen, 1947; Heusser, 1965), show a major expansion of *Picea sitchensis* during the last glacial period, which suggests moist and cold conditions at that time. Such conditions are also proposed by Heusser (1964) for the corresponding late Glacial of the Olympic Peninsula. However, it is possible that *Picea englemannii* spread to the west side of the Cascades during the last glacial as well, as Hansen (1947) has identified this as the species of *Picea* abundantly represented in the basal levels of the Scotts Mills profile in the Cascade foothills east of Salem, Oregon, and at Lake Kachess in the central Washington Cascades at an elevation of 670 m. Heusser (1964) interpreted the high grass levels of his GL-2 Zone at Humptulips, Washington, which probably represents early Wisconsin glaciation, as being indicative of cold, dry conditions. This zone is interpreted by Heusser as marking the most intense glacial conditions of the past 50,000 years. It seems likely that the LOK-1 assemblage derives from this event or one of similar magnitude, since geomorphic and palynological observations together indicate an intense glacial event accompanied by probable drier climatic conditions.

The record of *Quercus?* pollen is problematic. Its occurrence in a spectrum otherwise clearly subalpine may be explained either as a) *Q. garrayana*, which normally occupies lowland dry sites such as Willamette Valley, but is also found at elevations up to about 1500 m on dry south facing cliffs and rocky slopes near the top of Lookout Mountain (G. M. Hawk and J. F. Franklin, pers. comm.) approximately 15 km east of the LOK-1 site; or b) as evidence for past occurrence in the Cascades of one of the subalpine oaks, *Q. saddleriana* or *Q. vaccinifolia* now restricted in Oregon to the Siskiyou Mountains; or c) as representing another taxon.

Gold Lake Bog Research Natural Area (Franklin, 1972) at 1463 m elevation in the Willamette Pass area of the central eastern Cascades may provide a modern analogue of the type of vegetation which produced much of the pollen rain to LOK-1. This *Abies lasiocarpa-Picea englemannii* dominated stand is located approximately 60 km south of the Lookout Creek drainage. Low lying forests bordering marshes and bogs are typically dominated by *Picea englemannii* and *Abies lasiocarpa*. However, reproduction is mostly *Abies amabilis* (J. F. Franklin, pers. comm.) and adjacent upland sites (1650 m elevation) are mixed with *Tsuga mertensiana, Abies magnifica* var. *shastensis, Pseudotsuga menziesii*, and *Pinus monticola* (Franklin and Dyrness, 1973).

Although the forest at Gold Lake Bog differs in several respects from a forest which would yield a pollen assemblage like that of LOK-1, such as the low importance of *Pinus contorta* and *P. albicaulis* and the high importance of *Tsuga mertensiana* in that area, it is useful as a site for evaluation of minimum vegetation displacement in the central Cascades of Oregon. This site, which is low in the subalpine zone (*Tsuga mertensiana* Zone of Franklin and Dyrness, 1973), is 1040 m above the LOK locality.

Carver (1973) and Scott (1977) present data for changes in equilibrium line altitude (ELA) during the late Quaternary glaciations in the Cascade Range based on study of glacial deposits and landforms. They conclude that the maximum late

glacial ELA depression was 950-1000 m in the Mt. Jefferson area (Scott, 1977) and 1025 m in the Mt. McLoughlin area (Carver, 1973). The more extensive presumed early Wisconsin glaciation depressed the ELA 1100 to 1150 m in these areas. These data are in good agreement with the magnitude of altitudinal displacement of vegetation inferred from analysis of the Lookout Creek assemblage.


#### Summary

In the valley of Lookout Creek, a diamicton of presumed debris torrent origin contains a variety of plant macro- and microfossils representative of valley bottom and upslope Pleistocene forests. Locality LOK-1 within the deposit appears to have preserved a small piece of forest floor litter consisting of abundant leaves, twigs, and wood of *Abies lasiocarpa.* It has yielded a pollen and spore assemblage rich in *Picea* cf. *englemannii* and *Abies* cf. *lasiocarpa.* Dispersed in the deposit at locality LOK-2 are other wood specimens, some of which show abrasion and rounding indicative of transport. These have been determined as *Abies* sp., *Pseudotsuga menziesii*, and *Thuja plicata*, the latter two being species of generally warmer requirements than the other species represented in the deposit. These fossils suggest the occurrence of *Picea englemannii/Abies lasiocarpa* forest in a cold valley bottom surrounded by more xeric communities on adjacent hillslopes. Similar ecological situations commonly occur today in the eastern slopes of the Washington Cascades.

A somewhat similar localized association in the Oregon Cascades is found in the Gold Lake Bog Research Natural Area at an elevation 1040 m above the Lookout Creek localities. This estimate of vegetation displacement is consistent with estimates of maximum equilibrium line altitude depression during glaciations in the Oregon Cascades. The Lookout Creek assemblage is probably of Late Pleistocene age and may have formed during Early Wisconsin or a previous glaciation under conditions significantly drier than those prevailing during late Wisconsin glaciation.



#### Acknowledgments

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In addition, the Trustees and Members approved an increase of individual and institutional memberships for 1982. Regular memberships will be $14 and student membership will be $8. A $1 discount will be given for membership paid before January 15.

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# Use of Polar Coordinates in Random Sampling[2]

**Abstract**

A method is presented that allows field workers to locate random points quickly through the conversion of Cartesian coordinates to polar coordinates using a pocket calculator.

## Introduction

In sampling natural populations for a given attribute (e.g., density), randomness must be introduced into the sample design if estimates of error are to be assessed and valid conclusions obtained. This concept of randomness is now generally accepted by ecologists. There are numerous examples every year in ecological research, however, in which samples are collected using either a convenience or a judgment selection process (Lapin, 1975) in spite of the limitations inherent in such a strategy. Paramount among the justifications for such sampling is the apparent belief that, in some circumstances, estimates of the mean will deviate less from the true value than comparable estimates given by random samples (Greig-Smith, 1964), and a conviction that random sampling is too complex and time consuming (Cochran, 1963).

In this paper, we present a simple method that allows a field worker to locate sampling points using a systematic technique; i.e., by moving a given distance ($r$) in a given direction ($\alpha$). This technique diminishes the basis for the argument against random sampling that it is inefficient. The other criticism, less deviation from the mean, has been shown to be only marginally valid at best (Bourdeau, 1953).

When a population is being sampled randomly, every possible sample point in the population has an equal probability of being selected. Accomplishment of this goal is not as elementary as is sometimes believed. For example, the customary manner of throwing a quadrat in some arbitrary direction as a way of achieving random observations is ineffectual (Greig-Smith, 1964). A systematic random sample, in which the first sample point is selected randomly and the remainder are chosen at even-spaced intervals, is also prone to sampling bias, especially if the interval coincides with natural periodic variation (Cochran, 1963).

One way to obtain random samples has been through the use of Cartesian coordinates.

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This function requires that orthogonal axes be constructed in a manner that all possible sample points in the population are contained in the plane defined by the two axes. To locate a sample point, a value is randomly selected for each axis. The sample point is then located by going along one axis to the value chosen for it and then traversing at a right angle a distance equal to the value selected for the second axis. It is generally necessary to return to the first axis or the origin of the two axes before locating the next sample point. Thus, substantial time and effort are wasted between location of sample points.

#### Conversion to Polar Coordinates

An alternative way of defining the location of points on a plane is through the use of polar coordinates. Using this system, the location of a point is defined in terms of a distance from the origin (r) and a directed angle from an initial ray emitting from that origin ($\Theta$). The following equations and Figure 1 illustrate the relationship between Cartesian and polar coordinates.

$$x = r \cos \Theta$$

$$y = r \sin \Theta$$

Thus,

$$r = \sqrt{x^2 + y^2} \qquad (1)$$

$$\Theta = \tan^{-1} y/x \qquad (2)$$

where: x and y are Cartesian coordinates

r is the distance from the origin (0,0) to the point defined by Cartesian coordinates (x,y)

$\Theta$ is an angle between 0 and 90 degrees.

Although a sample point location is defined with respect to a Cartesian coordinate system, polar coordinates could be used to define the location of the next sample point in terms of the location of the current sample point. Thus, an individual need not return to an axis or the origin of both axes before locating the next sample point, which could result in a substantial savings of time and effort.

The location of the next sample point in terms of the location of the current sample point can be accomplished in the following manner and is illustrated in Figure 2. The horizontal and vertical distance between the location of the current and the next sample point can be computed as follows:

$$\Delta x = x_{j+1} - x_j \qquad (3)$$

$$\Delta y = y_{j+1} - y_j \qquad (4)$$

where: $(x_{j+1}, y_{j+1})$ is the Cartesian coordinate associated with the next sample point location.

$(x_j, y_j)$ is the Cartesian coordinate associated with the current sample point location.

Equation 1 can be used to express $\Delta x$ and $\Delta y$ in terms of a polar coordinate distance (r). Equation 2 and Table 1 can be used to define a bearing ($\propto$) from the current sample point location to the next sample point location. This table assumes magnetic north is used as the initial ray. Therefore, the angle being measured is with respect to the vertical axis of the Cartesian coordinate system (Fig. 2).

TABLE 1. Computation of the bearing from the current sample point location to the next sample point location.

| If the sign of | | The bearing |
|---|---|---|
| x computed using equation 3 is | y computed using equation 4 is | $\alpha$[1] is |
| positive | positive | $\lvert\theta\rvert$[2] |
| negative | positive | $180 - \lvert\theta\rvert$ |
| negative | negative | $180 - \lvert\theta\rvert$ |
| positive | negative | $360 - \lvert\theta\rvert$ |

[1]Azimuth in degrees.
[2]Absolute value of $\theta$ computed using Equation 2.

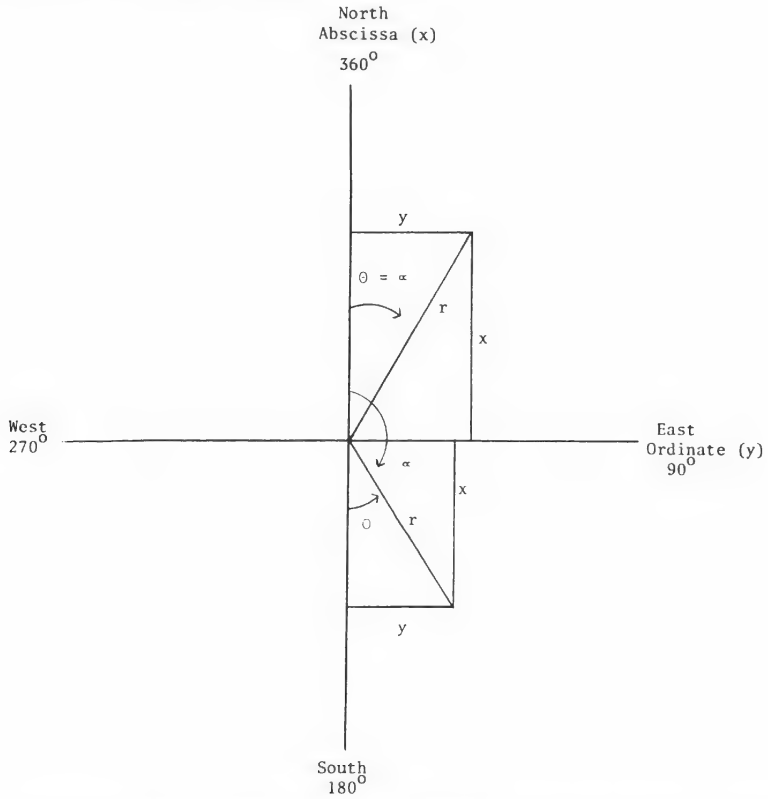


Figure 1. Example of relationship between polar and Cartesian coordinate system for two points in the 1st and 2nd quadrats, respectively.

### Sample Point Location Generation

If every possible sample point in the population is to have an equal probability of selection, values along the X and Y axes must all have the same chance of being selected. This can be accomplished through the use of a random number table. A pocket

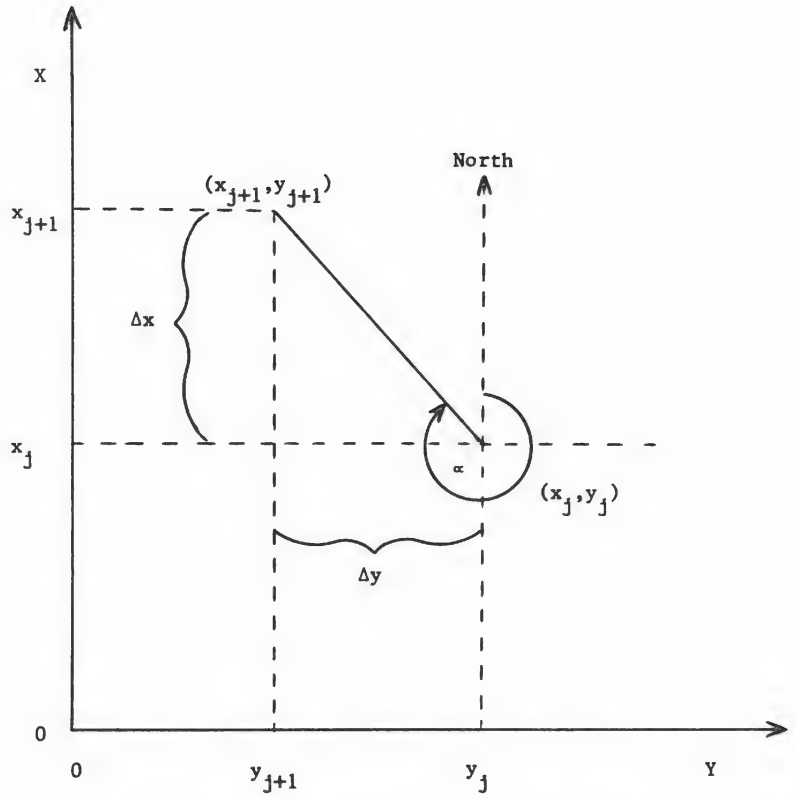


Figure 2. Geometric depiction of use of polar coordinates to locate the next sample point with respect to the present sample point.

calculator is also capable of generating uniformly distributed pseudorandom numbers.[3] The numbers lie in the interval 0 to 1 and are generated through the use of the following recurrence relationship (Martin, 1968):

$$U_{i+1} = KU_i$$

where: $K = 8t \pm 3$

t is a positive nonzero integer

$U_i$ is the last decimal number generated between 0 and 1. When initialized it should be an odd value.

$U_{i+1}$ is the least significant part of $K \cdot U_i$ and is the next decimal number generated between 0 and 1.

By multiplying U times the length of a Cartesian axis (X), a value along the X axis is randomly generated from a uniform distribution.

[3]Hewlett-Packard HP-45 Application Book, Hewlett-Packard Co., 1974, p. 165.

### Sample Point Location Procedure

The preceding relationships enable a field worker to generate his next sample point location randomly and walk directly to it from his current location. To perform the necessary calculations, a pocket calculator with at least an arctangent and square root function key and one constant storage register is required. The procedure, which is presented in detail in Table 2, entails generating the Cartesian coordinates associated with the next sample point location and computing both the distance and the bearing to the next sample point location. With this information, the individual can proceed to the next sample point location. The distance can be paced or, preferably, measured with a tape and the bearing maintained through the use of a hand compass.

TABLE 2. Procedures for the selection and location of the next sample point.

| Step No. | Equation No. | Description of Step |
|---|---|---|
| 1 | 5 | Generate the next value of U ($U_{i+1}$) |
| 2 | | Compute $x_{j+1} = U_{i+1} \bullet$ (maximum value of the x axis) |
| 3 | 5 | Generate the next value of U ($U_{i+2}$) |
| 4 | | compute $y_{j+1} = U_{i+2} \bullet$ (maximum value of the y axis) |
| 5 | 3 | Compute $\Delta x$ |
| 6 | 4 | Compute $\Delta y$ |
| 7 | 2 | Compute $\Theta$ |
| 8 | | Use Table 1 and results of Steps 5, 6, and 7 to compute $\propto$ |
| 9 | 1 | Compute r |
| 10 | | Proceed to the next sample point location |
| 11 | | If another sample point location is desired, repeat Steps 1 through 10. |

### Discussion and Conclusions

The technique described above is not without limitations. Rugged terrain and/or heavy overstory vegetation could preclude locating predetermined sampling points by a sighting and pacing system. However, such conditions would also preclude the ground location of predetermined sampling points by alternative point location procedures.

The magnitude of any biases which might be inherent in using a polar coordinate system in comparison with a Cartesian coordinate system has not yet been assessed. One would expect to find no difference since similar measure problems exist with both methods. Furthermore, regardless of the system used, measurement to sample point locations need not be exact to retain the principle of randomness (Greig-Smith, 1964).

It is possible to generate random values of r and $\Theta$ directly using procedures set forth in this paper. However, it should be noted that if sample point locations are selected using values of r and $\Theta$ randomly generated in this manner, not all possible sample point locations have the same probability of selection. Consequently, that method is not recommended.

This procedure works well for areas which are rectangular or square in shape. It is possible to implement the procedure in areas of other shapes, but randomly selected sample point locations falling outside the area must be rejected. Frequent replacement of rejected sample point locations can make the procedure somewhat inefficient.

If the area being sampled is large or has an irregular boundary, considerable time might be saved through selecting random coordinates in advance and ordering them in a sequence, thus minimizing the total distance traveled. For large sample sizes, a computer-generated numerical solution would be best (Ashley and Beers, 1972).

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# Contributions to the Life History of the Shorthead Sculpin, Cottus confusus, in the Big Lost River, Idaho: Age, Growth, and Fecundity

**Abstract**

Age, growth, and fecundity were examined for 513 shorthead sculpin, *Cottus confusus*, collected from the Big Lost River, Idaho. Age determination by otoliths revealed six age classes, with growth being fastest the first year (33 mm) and slowing to approximately 10 to 12 mm a year thereafter. Age class composition and condition varied with the habitat. Condition also fluctuated seasonally. Fecundity ranged from 184 to 511 eggs and was proportional to length.

## Introduction

The shorthead sculpin, *Cottus confusus*, occurs mainly in the Puget Sound and Columbia River drainages (Bailey and Bond, 1963); it also occurs in the isolated Lost River system. The occurrence of *C. confusus* in the Big Lost River can be attributed to an ancestoral connection between the Lost and the Snake Rivers. Sculpin are of little economic importance, but their abundance in most western streams (MacPhee, 1966) makes understanding their life history necessary in order to understand these stream systems.

Distribution patterns suggest that competition may exist between *C. confusus* and other sculpin, thereby limiting the downstream migration of *C. confusus* or the upstream migration of other sculpin (Maughan and Saul, 1979). This limited distribution has also resulted in the placement of *C. confusus* on the rare or endangered species list of Canadian fishes (McAllister, 1970). Specific data on the life history of the species are inadequate in many areas. The purpose of this paper is to describe the age, growth, and fecundity of *C. confusus*.

## Methods and Materials

The study was conducted on a section of the Big Lost River which runs through the Idaho National Engineering Laboratory (INEL) (Andrews, 1972; Overton and Johnson, 1976). The results are based on 513 shorthead sculpin collected in the autumn of 1976 and the spring of 1977 by means of AC and DC electrofishing gear.

The autumn collection (25 September and 2 and 3 October 1976) was made over a 2 km section of the river below the INEL diversion dam. The spring sample (13 and 24 April 1977) was restricted to three sampling stations immediately below the

INEL diversion dam because of low water. These three sampling stations appeared to be representative of the major habitats found in that portion of the river. Site one consisted of deep fast water with a boulder and fine gravel substrate, race. Site two was shallow water with moderate current, and fine gravel and marl substrate, riffle. Site three was of moderate depth, with slow current and fine gravel interspersed with large boulders, pool-rubble area.

Standard and total lengths of preserved specimens were taken to the nearest 1 mm and weight to the nearest 0.1 gram. Otoliths were removed and sex determined by dissection. Age was determined by examination of otoliths (Bailey, 1952). Calculated lengths to the time of annulus completion were determined by the formula, $L = F + (SL - F/R_0)Ra$, where L is the calculated standard length, F is the L-intercept as calculated by a linear regression of standard length and otolith radius, $R_a$ is the otolith radius in ocular micrometer units from the focus to the annulus, $R_0$ is the otolith radius in ocular micrometer units from the focus to the anterior margin of the otolith, and SL is the standard length (Everhart *et al.*, 1975).

Condition coefficients were calculated by the formula, $K = 10^5\ W/L^3$, after Lagler (1952), where K is the condition coefficient, W is the weight in grams, and L is the total length in mm. Total length was used for the determination of conditions to produce results of the same magnitude as other published accounts of condition. The relationship between total and standard length can be described by the formula, $SL = 0.53 + 0.79$ TL. Condition was analyzed by sex, age, size, season, and sample location using analysis of variance and multiple range testing (Zar, 1974).

Fecundity was measured by direct count of ova. The relationships between fecundity and standard length, weight, age, and condition were established by linear, exponential, and multilinear regression analysis, respectively (Zar, 1974).

## Results

The determination of age by examination of otoliths revealed 6 year classes (Table 1). The relationship between the standard length of the sculpin and the anterior radius of the otolith was determined to be a linear regression with a correlation coefficient of 0.95. This strong relationship adds validity to the use of otoliths as an aging tool and allows the determination of a correction factor (–1.52 mm). The relationship can be described by the formula, $SL = 1.34\ R_a - 1.52$.

TABLE 1. Calculated standard lengths at annulus formation of **Cottus confusus** in the Big Lost River, Idaho.

| Year Class | Number of fish | Annulus Number | | | | |
|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 |
| 1976 | 92 | | | | | |
| 1975 | 63 | 33.9 | | | | |
| 1974 | 50 | 34.2 | 46.9 | | | |
| 1973 | 44 | 32.6 | 44.4 | 56.1 | | |
| 1972 | 26 | 29.5 | 41.0 | 54.2 | 66.1 | |
| 1971 | 14 | 34.7 | 45.3 | 54.0 | 66.1 | 77.5 |
| Weighted mean length at annulus formation | | 33.2 | 44.7 | 55.1 | 66.1 | 77.5 |
| Mean annual growth | | 33.2 | 11.5 | 10.4 | 11.0 | 11.4 |

Sculpin attain a length of approximately 33 mm SL during the first year, after which growth slows to approximately 10 to 12 mm a year (Table 1). Growth of the population from October through mid-April, if the two samples are taken to be representative of the population as a whole, was 2.9 to 5.4 mm. This growth represents approximately 11 to 47 percent of the mean annual growth (Table 2).

TABLE 2. Mean standard length at capture, and growth of **Cottus confusus** from October through mid-April in the Big Lost River, Idaho.

| | Autumn | | Spring | | | |
|---|---|---|---|---|---|---|
| Age Class | Length Mean | Number of Fish | Mean Length | Number of Fish | Growth (mm) Autumn-Spring | % of Mean Annual Growth |
| 1 | 34.4 | 14 | 38.0 | 78 | 3.6 | 11 |
| 2 | 43.8 | 6 | 46.7 | 57 | 2.9 | 25 |
| 3 | 55.8 | 6 | 58.9 | 44 | 3.1 | 30 |
| 4 | 66.1 | 23 | 70.7 | 21 | 4.6 | 42 |
| 5 | 76.7 | 14 | 82.1 | 12 | 5.4 | 47 |
| 6 | 87.4 | 9 | 91.0 | 5 | 3.6 | * |

*Percent of annual growth could not be determined because annulus had not yet formed.

The length-weight relationships were determined for three groups of sculpin: autumn 1976, pre-spawn 1977, and post-spawn 1977. Since no difference was observed between the sexes, as determined by analysis of covariance, data were combined. Growth relationships were of the allometric type following the general formula, $W = aL^b$, where a and b are empirically determined constants. The autumn sample can be represented by the formula $W = 9.36\ L^{3.25}(10^{-6})\ (r = 0.99)$, the pre-spawn sample by the formula, $W = 1.29\ L^{3.22}(10^{-5})\ (r = 0.99)$, and the post-spawn sample by the formula, $W = 3.43\ L^{2.97}(10^{-5})\ (r = 0.98)$. The relationships were statistically different ($P < 0.05$) at all levels, as determined by analysis of covariance.

An analysis of condition factors revealed no significant difference between the sexes, as determined by the Student t-test, so data were combined. Condition of age class in the spring sample revealed no significant differences. However, autumn conditions were significantly different by age class ($0.05 > P > 0.02$) with a trend for an increase in condition with an increase in age (Fig. 1). Likewise, size class—condition comparisons revealed no difference in the spring, but significant differences existed in the autumn, with a trend for condition to increase with size. Significant differences in condition also existed between the autumn and post-spawn spring sculpin, with the autumn sculpin exhibiting a lower relative condition; the effect was most pronounced in the smaller, younger fish.

Distinct habitats were sampled in the spring and fish collected in each area were characterized by relative condition and age class composition. Significant differences existed between habitats for condition and age, which suggests the lack of appreciable exchange between areas (Fig. 2). The race and riffle situations were similar in terms of age class composition, while the pool-rubble area had a significantly greater proportion of older fish ($0.02 > P > 0.01$). The pool-rubble area was assumed to be the spawning ground for the sculpin because of the high concentration of sexually ripe sculpin found in the pre-spawn sample; however, no actual spawning activity or egg clusters were observed. In terms of condition, the riffle and pool-rubble areas were

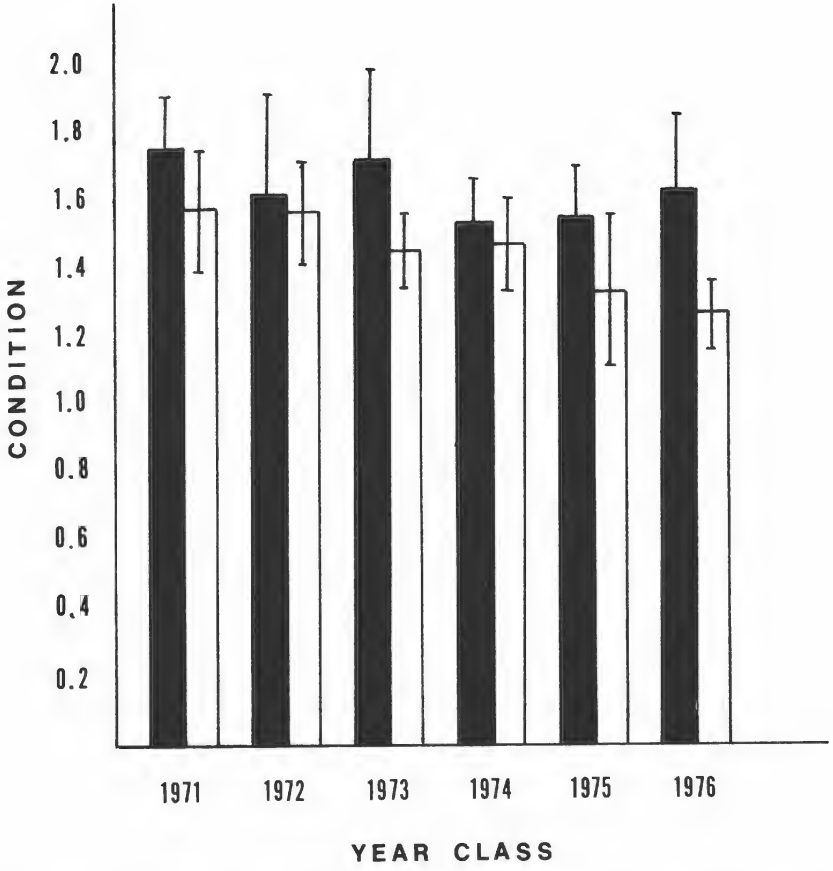


Figure 1. Condition-year class relationship for autumn and spring *C. confusus* in the Big Lost River, Idaho. Bars represent mean condition plus standard deviation, with black bars being spring and white bars being autumn.

similar, with the race situation producing a significantly lower condition ($0.01 > P > 0.005$).

The sculpin in the Big Lost River spawned over a very restricted time period; all females collected on 13 April 1977 were ripe, and females collected at the same location on 24 April 1977 were spent. This rapid spawn could be related to a dramatic reduction in water flow over this same period.

Twenty ripe females were collected in the pre-spawn sample and subjected to direct egg counts. Fecundity ranged from 184 eggs in a 53 mm 3 year old fish to 511 eggs in a 71 mm 4 year old fish. Age class 2 females were immature, and age classes 5 and 6 were not collected at that time. An analysis of the data revealed a linear relationship between the number of eggs and the standard body length to have the most significant correlation ($r = 0.91$) (Fig. 3). The relationship can be expressed by the formula, $F = 14.15\ SL - 531$, where F is the fecundity. Weight, age, and condition

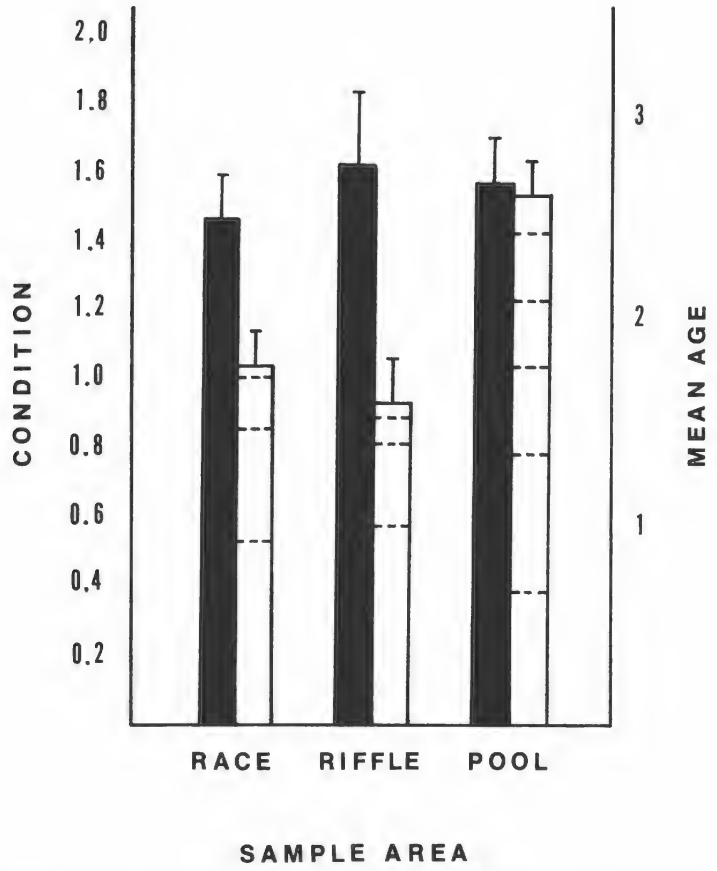


Figure 2. The relationship of condition and age class composition to habitat for *C. confusus* in the Big Lost River, Idaho. Black bars represent mean condition plus standard deviation; white bars represent mean age plus standard deviation. Dotted lines represent progressive year class proportions of the sample with the 1976 year class on the bottom.

did not exhibit an increased correlation to fecundity when analyzed by linear or exponential relationships. Correlation was not increased when analyzed by multilinear regressions involving length, age, and fecundity ($r = 0.85$), or length, weight, and fecundity ($r = 0.90$). No correlation was found between individual egg size (diameter and weight) and length, age, weight, or condition. These results establish length of individual fish to be the best predictive factor for fecundity of the shorthead sculpin in the Big Lost River.

#### Discussion

Growth of shorthead sculpin exhibited strong seasonal and age class relationships. There is a trend for the percentage of the mean annual growth occurring during the October through April period to increase with each age class (Table 2). This trend may follow

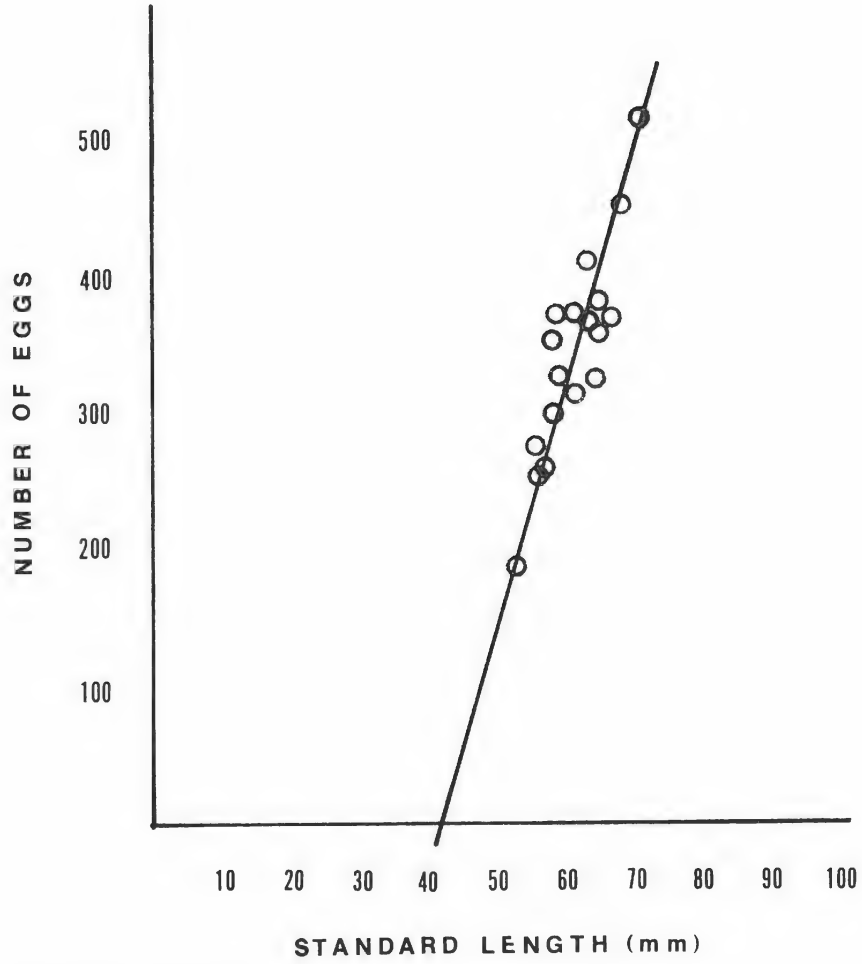


Figure 3. Length-fecundity of *C. confusus* in the Big Lost River, Idaho.

changes in the food habits of the different sizes of sculpin. Food habit data (Cannamela, Gasser, and Johnson, 1978) indicate that the majority of the October-April growth occurs in the early spring.

Weight and condition also varied seasonally and with age. The pre-spawn spring sample was significantly heavier after age 2, which was undoubtedly due to gonad development. Weight-condition differences were also significant between autumn and post-spawn spring sculpin. The increase observed from the autumn to post-spawn spring may be attributed to an increased feeding activity for the populations as a whole in the spring (Cannamela *et al.*, 1978). The more dramatic increase seen in the younger fish (year classes 1976, 1975, Fig. 1), may have resulted from increased food availability and high expenditures of energy for the formation of reproductive products in older fish during the pre-spawn period. The piute sculpin, *Cottus beldingii*,

also exhibits a seasonal fluctuation of condition which is likely related to gonadal development and food supply (Ebert and Summerfelt, 1969).

Relative food abundance could be a causative factor in the observed differences in condition between habitats; however, benthic samples taken in each habitat revealed no difference in food availability (Cannamela *et al.*, 1978). The physical characteristics of each habitat may be responsible for condition differences. The high current velocity in the race area could act to restrict foraging activity, or cause a greater expenditure of energy in terms of securing forage and maintaining position in the stream. This increased level of energy use would result in less energy available for growth.

Fecundity of shorthead sculpin from the Big Lost River was significantly higher than that reported elsewhere. Patten (1971) found fecundity to range from 47 in fish 61 mm long to 217 in 86 mm sculpin from two Washington streams. The factors which affect the fecundity of the shorthead sculpin are largely unknown; however, the degree of variation between the two areas suggests that regulatory cues have a strong influence.


#### Summary

The limited life history data for the shorthead sculpin have been supplemented by determination of the following from the Big Lost River population:

1) Otoliths for 6 year classes were analyzed and their validity for age and growth studies was confirmed for this species;

2) These sculpin grew 10-12 mm a year after reaching 33 mm at the end of their first year. The seasonal pattern of growth varied according to age with no sexual dimorphism;

3) Condition factors were higher in spring than autumn;

4) Spawning occurred in mid-April with fecundity positively correlated with fish length and ranging from 184 to 511 ova for 3- and 4-year-old fish; and

5) In the spring, reproductively mature fish were most common in pool-rubble habitat, while smaller fish were found in race and riffle areas.



#### Acknowledgments

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# Shallow-water Intertidal Ichthyofauna of the Yaquina Estuary, Oregon

**Abstract**

A 3.0 m beach seine was used to capture fishes in intertidal eelgrass (*Zostera marina*) or over intertidal mudflats in water 0.4-0.7 m deep. Thirty-two species and 42,096 fish were collected; 86 percent of the fish weighed under 5 g. Thirty species were collected in eelgrass but only twenty-three in the upper intertidal. In August, December, January, and May through July, more fish were collected in eelgrass; but from February through April, more fish were collected in the upper intertidal. A greater standing stock and more fishes were collected at night than during daylight in eelgrass and in the upper intertidal in August, but in December in eelgrass only the standing stock was greater in darkness. Some fish species (e.g., *Cymatogaster aggregata*) were more abundant at night, other species showed no differences in abundance, and a few species (e.g., *Syngnathus leptorhynchus*) were more abundant during daylight. Fishes weighing less than 1.5 g showed peak abundances from late winter through summer, but larger fishes showed peak abundances only in summer.

## Introduction

There have been numerous Pacific Northwest estuarine ichthyofaunal surveys (see partial review in Bayer, 1979b), especially in Oregon (Haertel and Osterberg, 1967; Beardsley, 1969; Cummings and Schwartz, 1971; Demory *et al.* 1973; Cummings and Berry, 1974; Swartz *et al.*, 1974; Johnson in Pearcy and Myers, 1974; Higley and Holton, 1975; Hostick, 1975; Stout, 1976; Durkin *et al.*, 1977; Forsberg *et al.*, 1977; Durkin *et al.*, 1979; Myers, 1980). However, these studies have either not sampled the intertidal, did not distinguish between intertidal and subtidal collections, and/or did not state the part of the water column sampled.

Here, I examine intertidal fish assemblages in shallow water ($< 1$ m) in a persistent eelgrass (*Zostera marina*) bed and in the upper intertidal at the Yaquina estuary, Oregon. Elsewhere, I discuss Yaquina eelgrass inertidal zonation (Bayer, 1980b), aspects of the biology of the intertidal fishes *Aulorhynchus flavidus* (Bayer, 1980c), *Syngnathus leptorhynchus* (Bayer, 1980a), *Cymatogaster aggregata* (Bayer, 1979b), *Lumpenus sagitta* (Bayer, 1979b), and *Leptocottus armatus* (Bayer, 1979b); the length-frequencies, densities, and standing stocks of Yaquina intertidal fishes (Bayer, 1979b), and the presence of selected Yaquina shallow-water intertidal macroinvertebrates (Bayer, 1979b).

## Study Area and Methods

The 15.8 km$^2$ Yaquina estuary (44° 38′N, 124° 03′W) is a drowned river valley located on the central Oregon coast. The tidal regime of Oregon estuaries is semi-diurnal mixed with approximately 6 h between tides. Mean Higher High Water (MHHW), Mean High Water (MHW), Mean Tide Level (MTL), and Mean Low Water (MLW) are 2.55, 2.32, 1.40, and 0.47 m above Mean Lower Low Water (MLLW), respectively (Oregon State Land Board, 1973).

From August 1975 to July 1976, a beach seine 3.0 m long and 1.1 m high with a 10 mm stretched mesh was used to capture macrofauna. August seining was at A, but all other collections were at B (Fig. 1). Seining was at two different tidal elevations within the two intertidal zones: the upper intertidal (+0.9 to +1.3 m above MLLW) over mudflats, and the lower intertidal (−0.2 to +0.4 m above MLLW) in a persistent eelgrass bed (Bayer, 1980b). Tidal elevation was noted before seining at the Oregon State University tide recorder, which was adjacent to the study area (Fig. 1). In eelgrass, a seine designed to prevent rolling (Bayer, 1979b) was used; it was of the same dimensions and was pulled through the water at the same velocity as the seine used at higher tide heights. One sample consisted of a series of 10 hauls,

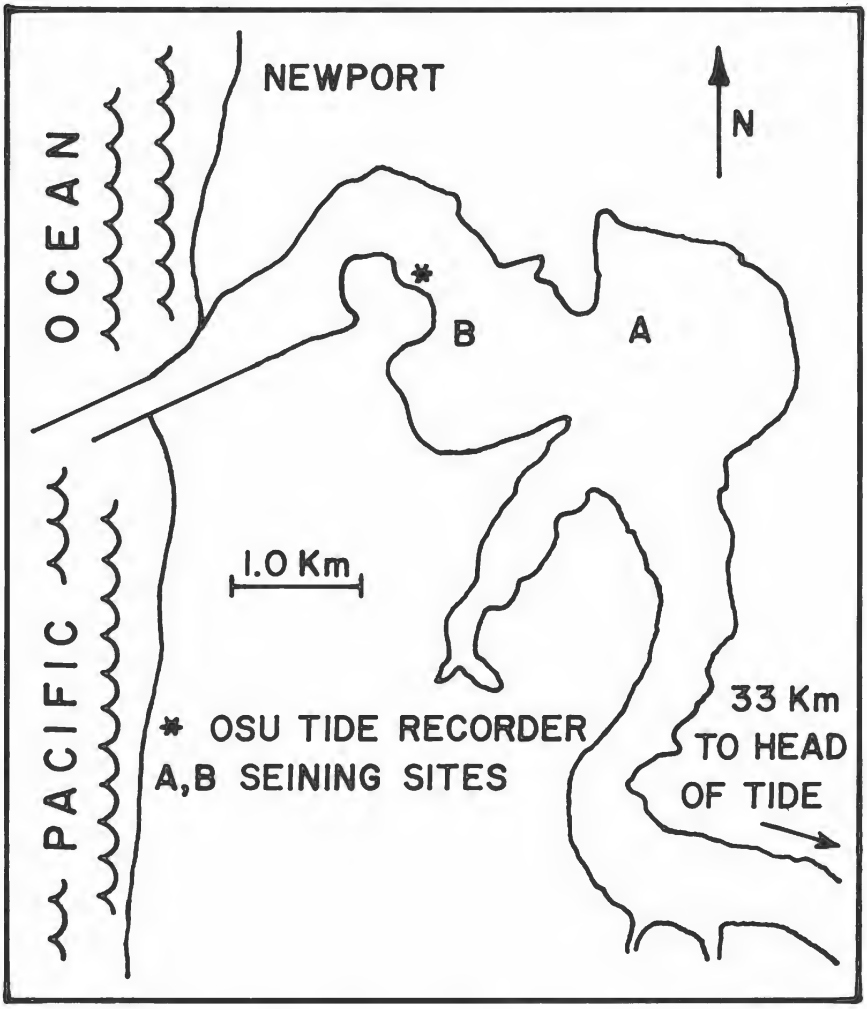


Figure 1. Lower Yaquina estuary showing August (A) and September through July (B) sampling areas.

each approximately 30 m long. Seine velocity was about 0.5 m/sec in water 0.4-0.7 m deep. At upper intertidal elevations, the seine was pulled to shore at termination of a haul, but in eelgrass, the amount of macrophyton sometimes caught in the seine made termination in water necessary. The area covered in a sample was approximately 600 sq. m.

In collections where specimens of a fish species were numerous and about the same size (i.e., juvenile *Hypomesus pretiosus* in February through March, juvenile *Cymatogaster aggregata* in August through October and July, *Embiotoca lateralis* in August, *Sebastes melanops* in August, *Leptocottus armatus* less than 40 mm from January through May, and *Parophrys vetulus* less than 40 mm from December through June), all similar-sized fish were counted, and total lengths (TL) and wet weights of at least 100 fish of each species in each collection were recorded. The average wet weight of fish in the collection was then assigned to other similar sized fish of that species. However, for most species, the total length was recorded for all fish. The wet weights of most individuals were also recorded, and for those individuals not weighed, a weight was estimated using a length-wet weight curve. All length measurements are total length unless otherwise noted.

## Results

### Size

A total of 42,096 fish weighing about 133.4 kg were collected. Species collected are listed in Table 1. The largest fish collected was a 413 mm, 1.11 kg *P. stellatus* while the shortest fish collected was a 15 mm *P. vetulus* weighing less than 0.2 g. For 11 species, some individuals weighed less than 0.2 g. Most fish (86 percent) and more species (30) weighed less than 5 g than over 5 g (Table 1), but fish weighing less than 5 g contributed only 49 percent of the total biomass. Only 10 species had individuals weighing over 25 g, with *L. armatus* and *P. stellatus* constituting most of the fish over 25 g (48 and 27 percent in eelgrass, respectively; 68 and 27 percent in the upper intertidal, respectively).

### Habitat

More species throughout the year (Fig. 2) were collected in eelgrass than in the upper intertidal. Nine species were collected only in eelgrass (Table 1). Two species were collected only in the upper intertidal, but these species were represented by only one or two fish (Table 1).

Although differences in seining techniques might have resulted in differences in total catch, differences in total catch between eelgrass and the upper intertidal were not consistent. In August, a greater average standing stock (Fig. 3) and significantly more fish at night ($t = 7.33$, $P < .01$) and during daylight ($t = 3.47$, $P < .01$) were collected in eelgrass than in the upper intertidal. Comparisons were not possible for September through November because eelgrass samples were made during darkness, but upper intertidal samples were during daylight (Fig. 2). But comparisons between eelgrass and the upper intertidal could be made during daylight throughout the rest of the study. In December, a greater average standing stock (Fig. 3) and significantly more fish ($t = 6.01$, $P < .01$) were collected in eelgrass than in the upper intertidal. In January, more fish (but not significantly more, $P > .10$) and

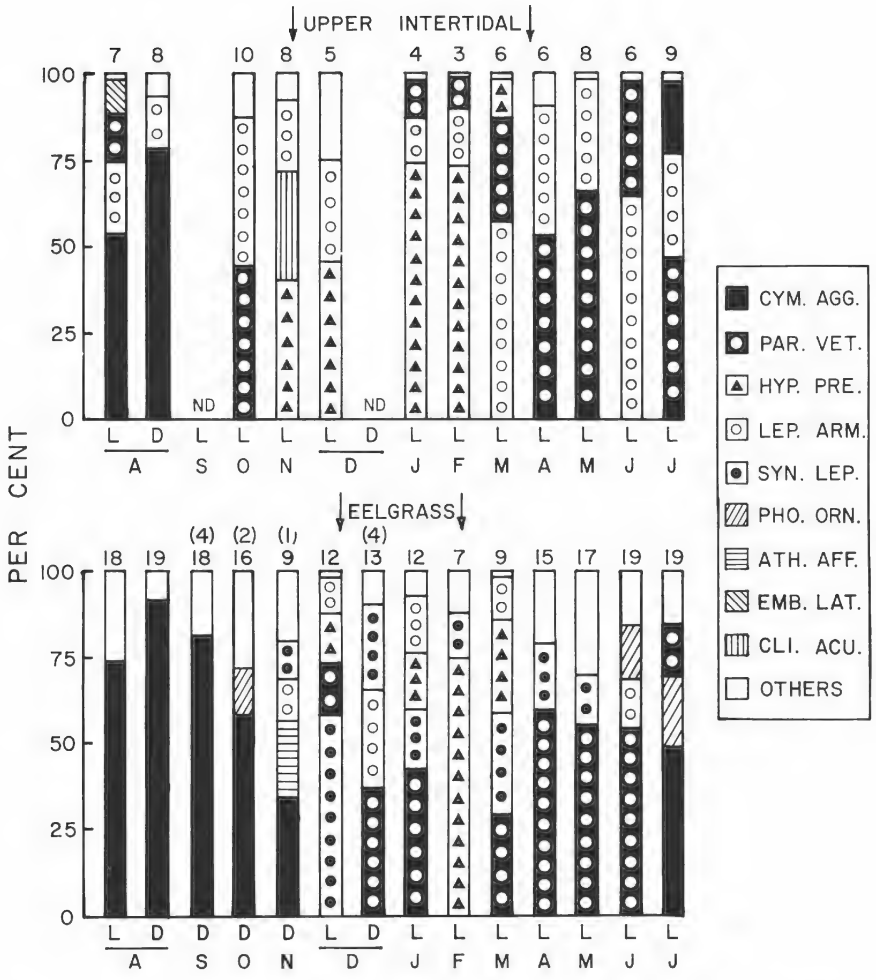


Figure 2. Relative dominance of fish species with 10 percent or more of total monthly catch. Number of samples collected per month above the monthly relative dominance bar. Species abbreviations from Table 1. Collections during light (L) or darkness (D). Number of samples, if different from five, in parentheses above number of species. ND = No Data.

a greater standing stock (Fig. 3) were again collected in eelgrass. From February through April, more fish were collected in the upper intertidal, but the difference was not significant ($P > .10$). In contrast, a greater average standing stock was collected in eelgrass in February and April; only in March was a greater standing stock collected in the upper intertidal (Fig. 3). From May through July in eelgrass, more fish (but not significantly, $P > .10$) and a greater average standing stock (Fig. 3) were collected.

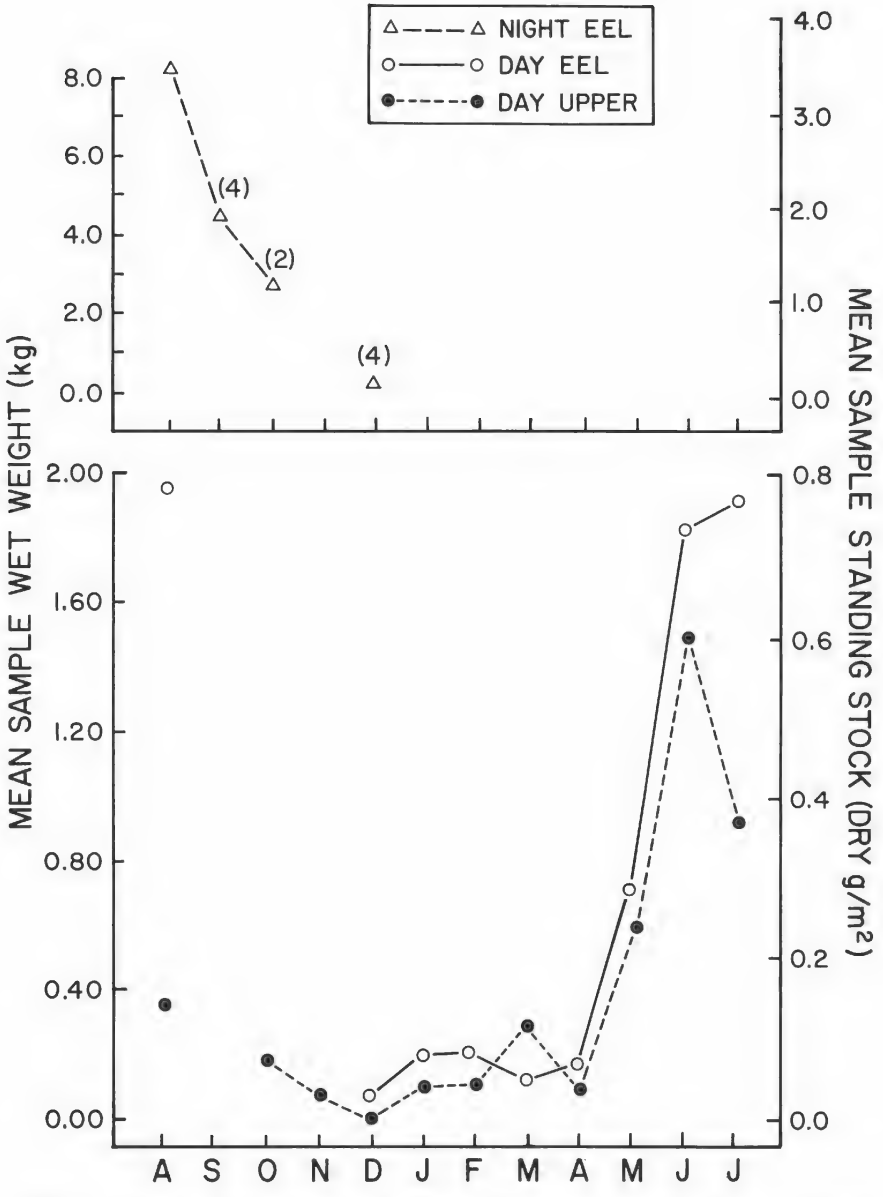


Figure 3. Mean wet weights and mean dry standing stocks. Number of samples, if different from five, in parentheses. Dry weight = 0.25 wet weight, based on the average found by Thayer *et al.* (1973).

TABLE 1. Fish species, number captured, weight-class, habitat, total length range, and months of capture from August 1975 through July 1976. Those not collected in eelgrass (EEL) were collected in the upper intertidal.

| | N | Fish <5 g (%) | Fish in EEL (%) | TL (mm) | Captured Months |
|---|---|---|---|---|---|
| **Clupea harengus** | 28 | 100 | 75 | 29-46 | IV-VII |
| **Engraulis mordax** | 6 | 100 | 100 | 88-97 | VIII-IX |
| **Oncorhynchus keta** | 43 | 100 | 98 | 50-55 | IV-V |
| **O. kisutch** | 4 | 25 | 100 | 67-137 | VIII,VI-VII |
| **O. tshawytscha** | 2 | 100 | 50 | 38-42 | I,III |
| **Hypomesus pretiosus** | 3162 | 100 | 44 | 37-87 | XI-V |
| **Atherinops affinis** | 31 | 84 | 55 | 65-123 | XI-I,VII |
| **Aulorhynchus flavidus** | 135 | 93 | 97 | 27-188 | VIII-VII |
| **Gasterosteus aculeatus** | 37 | 100 | 95 | 24-62 | VIII-I,V-VII |
| **Syngnathus leptorhynchus** | 1069 | 93 | 99 | 67-385 | VIII-VII |
| **Cymatogaster aggregata** | 22171 | 95 | 95 | 39-150 | VIII-I,IV-VII |
| **Embiotoca lateralis** | 960 | 4 | 95 | 70-108 | VIII-IX,VI-VII |
| **Hyperprosopon argenteum** | 2 | 100 | 0 | 60 | VI-VII |
| **Phanerodon furcatus** | 23 | 30 | 91 | 67-90 | VIII |
| **Rhacochilus vacca** | 7 | 0 | 100 | 83-90 | VIII |
| **Anoplarchus purpurescens** | 1 | 100 | 0 | 58 | XI |
| **Lumpenus sagitta** | 342 | 11 | 94 | 86-395 | VIII-IX,IV-VII |
| **Apodichthys flavidus** | 52 | 62 | 100 | 31-215 | VIII-VII |
| **Pholis ornata** | 1242 | 60 | 98 | 35-178 | VIII-X,XII-I,IV-VII |
| **Sebastes caurinus** | 82 | 99 | 100 | 19-80 | VIII-X,VI-VII |
| **S. melanops** | 1026 | 96 | 99 | 38-92 | VIII-X,IV-VII |
| **Hexagrammos decagrammus** | 316 | 31 | 100 | 50-148 | VIII-X,XII,III-VII |
| **Ophiodon elongatus** | 3 | 0 | 100 | 166-250 | VIII-IX |
| **Blepsias cirrhosus** | 22 | 95 | 100 | 27-87 | X,IV-VI |
| **Clinocottus acuticeps** | 175 | 100 | 51 | 17-60 | VIII-VII |
| **Enophrys bison** | 5 | 20 | 100 | 31-120 | X,V-VII |
| **Leptocottus armatus** | 4361 | 63 | 31 | 18-270 | VIII-VII |
| **Oligocottus maculosus** | 7 | 86 | 71 | 43-75 | IX-XII |
| **Scorpaenichthys marmoratus** | 17 | 47 | 94 | 47-160 | VIII-X,VI-VII |
| **Parophrys vetulus** | 6602 | 90 | 49 | 15-135 | VIII-VII |
| **Platichthys stellatus** | 166 | 13 | 77 | 44-413 | VIII-X,XII-I,III-VII |
| **Psettichthys melanostictus** | 3 | 100 | 66 | 30-31 | VII |

### Light/Dark Abundances

Approximately the same number of fish species were collected at night as during the day in August in eelgrass (19 vs 18), and in the upper intertidal (8 vs 7) (Fig. 2). In December, 13 species were collected during the day in eelgrass and 12 at night.

In August, four species were significantly more abundant in eelgrass during darkness, but no species was significantly more abundant during daylight (Table 2). In August, two species were significantly more abundant in the upper intertidal during darkness, but one species (*E. lateralis*) was more abundant during daylight. Thus, *E. lateralis* was significantly more abundant in the upper intertidal during daylight but in eelgrass at night (Table 2). In December, no species was significantly more abundant in eelgrass at night, but *S. leptorhynchus* was significantly more abundant during daylight (Table 2).

A significantly greater average number of fish per sample was seined during darkness than during daylight in August in eelgrass ($t = 6.68$, $P < .01$) and in the upper intertidal ($t = 1.88$, $P < .10$) but not in December in eelgrass ($t = 0.15$, $P > .10$).

TABLE 2. Average number of fish per sample and student t values for means of catches in darkness versus catches in light in eelgrass (EEL) or in the upper intertidal (UP) in August and December for those species in which 20 or more total individuals were seined. Five samples for each condition, except in darkness in eelgrass in December (N = 4). Positive t values denote a greater average number of fish collected in darkness.

| | August | | | | | | December | | |
|---|---|---|---|---|---|---|---|---|---|
| | EEL | | | UP | | | EEL | | |
| | Light $\bar{x}$ | Dark $\bar{x}$ | t | Light $\bar{x}$ | Dark $\bar{x}$ | t | Light $\bar{x}$ | Dark $\bar{x}$ | t |
| **H. pretiosus** | | | | | | | 6.4 | 0.0 | -0.93 |
| **S. leptorhynchus** | | | | | | | 25.8 | 12.5 | -2.38 |
| **C. aggregata** | 305.8 | 2792.4 | 6.13[1] | 29.6 | 174.6 | 2.54[1] | | | |
| **E. lateralis** | 12.0 | 146.0 | 2.70[1] | 5.8 | 0.0 | -3.79[1] | | | |
| **L. sagitta** | 0.8 | 38.8 | 2.53[1] | 0.0 | 3.6 | 2.79[1] | | | |
| **P. ornata** | 25.0 | 20.8 | -0.67 | | | | | | |
| **S. melanops** | 11.6 | 114.8 | 5.71[1] | | | | | | |
| **H. decagrammus** | 12.6 | 20.0 | 0.92 | | | | | | |
| **L. armatus** | 20.4 | 19.4 | -0.15 | 10.0 | 12.2 | 0.68 | 4.8 | 10.0 | 0.95 |
| **P. vetulus** | 11.6 | 44.4 | 2.13 | 7.2 | 10.8 | 0.37 | 3.2 | 18.3 | 1.79 |

[1] $p < .05$

### Seasonality

The number of species changed seasonally in eelgrass and in the upper intertidal with peak diversity in eelgrass in summer (19 species) and in the upper intertidal in fall (10 species) (Fig. 2). Minimum diversity occurred in February in eelgrass and the upper intertidal (7 and 3 species, respectively) (Fig. 2). The low number of species (9) in eelgrass in November may have resulted from only one sample.

Most species appeared in spring or summer and disappeared in fall and winter, but one species (*H. pretiosus*) was only present from November through May (Table 1, Bayer, 1979b).

Fish weighing less than 1.5 g were most abundant in eelgrass in August and from January through July, but most abundant in the upper intertidal from January through May (Fig. 4). The winter-spring abundance represented the appearance of young-of-the-year or juvenile fish, especially *H. pretiosus, P. vetulus*, and *L. armatus* (Bayer, 1979b). In contrast, fish weighing 1.5-4.9 g and over 5.0 g were most abundant in eelgrass in July and August, but in the upper intertidal, peak abundance was in June (Fig. 4).

Small fish ($< 1.5$ g) began increasing in January through March (Fig. 4), but the average standing stock did not increase greatly until May (Fig. 3). Minimum biomass occurred in December, and maximum biomass was reached in July-August in eelgrass and in June in the upper intertidal (Fig. 3).

### Fish Densities and Standing Stocks

*Eelgrass.* The mean diurnal August standing stock was 0.80 dry g/m$^2$ (Fig. 3) and the fish density, 0.70 fish/m$^2$, but the mean standing stock and fish density were

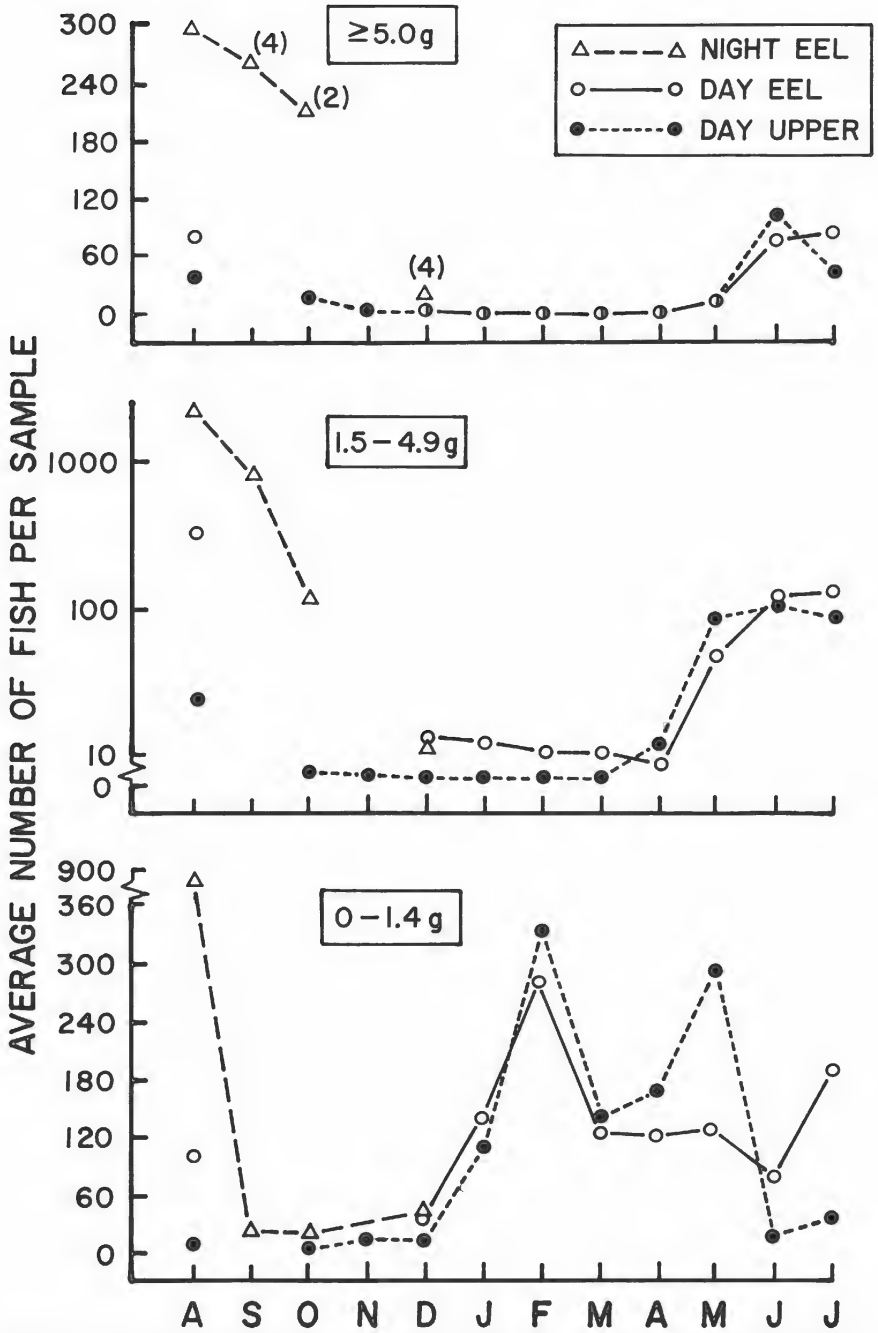


Figure 4. Average number of fish per sample per weight class. Number of samples, if different from five, in parentheses.

much greater during darkness (3.59 dry g/m$^2$, 5.28 fish/m$^2$). In December, the diurnal mean standing stock (0.03 dry g/m$^2$, Fig. 3) and fish density (0.08 fish/m$^2$) were less than in August, and the mean fish density was about the same during darkness. The December mean standing stock, however, was twice as great in darkness (0.06 dry g/m$^2$) as during daylight.

*Upper intertidal.* The mean diurnal August standing stock was 0.14 dry g/m$^2$ (Fig. 3), and the average fish density was 0.12 fish/m$^2$, but the mean standing stock (0.26 dry g/m$^2$, Fig. 3) and fish density (0.34 fish/m$^2$) were greater during darkness. The mean diurnal December density and standing stock were lower (0.02 fish/m$^2$, 0.01 dry g/m$^2$) than in August.

### Relative Abundance

Catches in eelgrass and in the upper intertidal were dominated by 1-4 species in numerical abundance (Fig. 2). In eelgrass, three species made up 75 percent or more of the monthly catch, but in the upper intertidal, two species made up 75 percent or more of the monthly catch throughout the study (Fig. 2). One species contributed over half of the total monthly catch in eelgrass for eight months and in the upper intertidal for seven months (Fig. 2). The monthly most dominant species in eelgrass were *C. aggregata, S. leptorhynchus, P. vetulus*, or *H. pretiosus*; but in the upper intertidal were *C. aggregata, L. armatus*, or *P. vetulus* (Fig. 2). Although some species were dominant in both eelgrass and in the upper intertidal, the species might not be dominant for the same months or for as long (Fig. 2).

*Eelgrass. C. aggregata* dominated the monthly catch from August through November and in July, and *P. vetulus* was dominant in January and March through June. Although *P. vetulus* and *C. aggregata* were dominant for an equal number of months, *P. vetulus* was a major contributor for eight months versus six months for *C. aggregata* (Fig. 2). *H. pretiosus* and *S. leptorhynchus* were dominant in February and December, respectively (Fig. 2).

*C. aggregata* was the most numerous species for fish less than 1.5 g (50 percent), over 1.5 g (71 percent), over 5 g (26 percent), and total fish (65 percent), but *L. armatus* was the most numerous species for fish weighing over 25 g (48 percent). In terms of biomass, *C. aggregata* was the main contributor (48 percent), followed by *L. armatus* (17 percent), and *P. vetulus* (7 percent).

Differences in relative abundance among species during light or darkness (Table 2) resulted in *C. aggregata* increasing its proportion of the total catch in August from 74 percent during daylight to 91 percent at night (Fig. 2). In December, both the dominant species and the rank order changed between light and darkness (Fig. 2). These changes might have resulted from *S. leptorhynchus* being significantly more abundant and *H. pretiosus* being slightly more abundant during daylight; but *P. vetulus* and *L. armatus* showed a less than significant increase in abundance during darkness (Table 2).

*Upper intertidal. C. aggregata* was the dominant species only in August (but note that there were no September samples) (Fig. 2). *P. vetulus* was dominant in October, April, May, and July; and *H. pretiosus* was dominant in November and December through February (Fig. 2). In March and June, *L. armatus* was dominant. In both

eelgrass and in the upper intertidal, *L. armatus* was the only species that contributed greatly to each monthly catch.

The most numerous species for fish weighing less than 1.5 g was *H. pretiosus* (49 percent), but *L. armatus* was the most numerous species for fish weighing more than 1.5 g (51 percent), more than 5 g (75 percent), more than 25 g (68 percent), and for total fish (45 percent). The major contributor to biomass was *L. armatus* (54 percent) followed by *P. vetulus* (20 percent) and *C. aggregata* (10 percent).

In August, *C. aggregata* was the dominant species both during daylight and during darkness, but *C. aggregata* increased its proportion of the total catch from 54 percent during daylight to 78 percent in darkness (Fig. 2).

## Discussion

### Intertidal/Subtidal Assemblages

Differences in gear and collecting techniques might account for differences in species abundance and presence between intertidal and subtidal macrofaunal collections. In this discussion, the intertidal and subtidal abundance of species will not be compared; but the presence of some species can be examined. Fast-swimming fishes such as members of the Clupeidae, Engraulidae, and Salmonidae have been previously found in Yaquina subtidal areas (Beardsley, 1969). Species of these taxa were rarely found in the intertidal during this study (Table 1), but they may have escaped the seine that I used or have been present in intertidal areas in water deeper than 1 m. For example, the presence of adult herring (*Clupea harengus*) in Yaquina intertidal areas was indicated by intertidal eelgrass covered with herring eggs (Bayer, 1980d).

However, differences in the intertidal/subtidal Yaquina distribution of species can be discerned for some slow-moving fishes, which would be most likely to be caught by all types of gear. Indeed, *E. bison* and juvenile *Citharichthys stigmaeus* were either rarely collected or were not collected in this study, but were commonly found in the Yaquina channel adjacent to the study area (Beardsley, 1969; Swartz *et al.*, 1974; Johnson in Pearcy and Myers, 1974). Thus, these species might have selected subtidal areas. Also, size-classes of a species might differ in intertidal/subtidal distribution. Small ($< 50$ mm) and larger *L. armatus* were common throughout the intertidal, but in the subtidal Yaquina channel, Beardsley (1969) and Burreson (1973) found few small *L. armatus*, although larger ones were common. Similarly, individuals of other cottid species were larger in subtidal than in intertidal areas (Beardsley, 1969; this study).

Yaquina intertidal fish assemblages might differ from adjacent subtidal assemblages because some fish (e.g., *L. armatus, P. stellatus*, and *P. vetulus*) follow tides (Kendall, 1966); or because some fish (e.g., *S. leptorhynchus*) were associated with eelgrass (Bayer, 1980a), and the densest growth of eelgrass was intertidal (pers. obs.). Selection for shallow waters by some fish is also indicated by the findings of Forsberg *et al.* (1977) at Tillamook Bay that *P. ornata, L. armatus, P. vetulus*, and *P. stellatus* were more abundant in shallow than deeper water.

### Intertidal Assemblages

Fish assemblages differed not only between subtidal and intertidal areas but also within the intertidal. Yaquina eelgrass beds contained more fish species and generally more

fish than the upper intertidal. Similarly, Tack (1970) found more fish species and more fish in eelgrass than over upper intertidal mudflats in Alaska in summer.

### Light/Dark Differences

At the Yaquina, species were either more abundant during daylight, during darkness, or did not differ in abundance between light and darkness (Table 2). Similarly, Kendall (1966) and McCleave and Fried (1975) found that species differed in abundance depending on light conditions. At the Yaquina, species differences in light/dark abundance (Table 2) resulted in differences in species' relative abundance between daylight and darkness (Fig. 2).

Nocturnal summer Yaquina fish densities in eelgrass averaged 7.5 times greater than daylight densities, and nocturnal standing stocks averaged 4.5 times greater than daylight standing stocks. Nocturnal summer fish densities in the upper intertidal averaged 2.8 times greater, and standing stocks 1.8 times greater than during daylight. In December, fish densities in eelgrass at night were about the same as during daylight, but standing stocks were twice as great at night. Similarly, Adams (1976) found throughout the year, on the average, a greater biomass at night in North Carolinian eelgrass beds, but McCleave and Fried (1975) found fewer fish at night in a Maine tidal cove.


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# Canopy Influence on Understory Community Composition

**Abstract**

Three tree and one shrub species (*Pinus ponderosa, Juniperus scopulorum, Quercus gambelii*, and *Ceanothus velutinus*) were chosen for this study. Ten individuals of each species were selected and their associated understory communities and adjacent open-area communities were sampled. The study site was in the lower Uinta Mountains about 16 k east of Kamas, Utah. Data taken included both biotic and abiotic parameters. Understory communities were found to differ significantly from each other and from adjacent open-area communities.

## Introduction

Curtis (1959) defines a community as a group of organisms which grow together in the same place and have mutual interactions. Trees and understory plants are both essential parts of the community; hence, postitive or negative interactions might be expected to develop between them. Differences in composition of plant communities which occupy understory and open habitats are easily recognized. Often overstory species affect cover (Anderson, 1969; McQueen, 1973; McConnell and Smith, 1970) and diversity of understory communities (Auclair and Goff, 1971). In addition, overstory species have been shown to be highly affected by soil improvement on the forest floor due to nitrogen fixation by such common understory plants as bitterbrush (*Purshia tridentata* (Pursh) DC.) and snowbrush ceanothus (*Ceanothus velutinus* Dougl.) (Wollam and Youngberg, 1964; Rusel and Evans, 1966; Webster, Youngberg, and Wollam, 1967). Anticipated growth of timber has been adversely affected by increases in understory vegetation (Gordon, 1962). Large herbaceous species have also been shown to modify their understory environment much the same as do trees (Smith and Cottam, 1967).

The most-studied environmental variable affecting understory communities is sunlight. Light intensity (del Moral, 1972) and spectral distribution (Federer and Tanner, 1966) strongly influence understory plant communities. Cline (1966) and Blackman (1956) have shown that the net assimilation rate of several herbaceous understory species tends to increase with light intensity. They have also shown that shading affects growth patterns in roots, shoots, and leaves, time spent in the vegetative

phase, and specific leaf area of some understory species. Other factors critical to development of understory communities are soil moisture and thickness of litter layer (Anderson *et al.*, 1969; McQueen, 1973).

The present study examines differences between understory (canopy-covered) and non-understory (open) plant communities of the forest floor as well as relationships between canopy species and their associated understory communities. We also examine the importance of canopy-influenced physical factors in separating understory communities associated with different canopy species.

### Study Area

The area of study is 16 k east of Kamas, Utah, along the Yellow Pine branch of Beaver Creek (111° 10′ W, 40° 38′ N). This area was chosen because of the homogeneous nature of the underlying parent material (an alluvial outwash gravel bed) throughout the site, its constant slope (10 percent) and exposure (185°), and its easy accessibility. The study area, as described by Cottam (1930), is an area of "zone jumbling," and contains plant representatives from all life zones except lower sonoran. The elevation of the site is 2200 m with an average annual precipitation of about 450 mm, 60 percent of which occurs in winter. It is an area of highly mixed vegetation varying from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.), white fir (*Abies concolor* Lindl.) and ponderosa pine (*Pinus ponderosa* Dougl.) to clumps of Gambel oak (*Quercus gambelii* Nutt.) and snowbrush ceanothus. Interspersed throughout the area are also individuals of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), quaking aspen (*Populus tremuloides* Michx.), and various other plant species. All can be found at approximately the same elevation and in fairly close proximity.

Because of its unique nature, the area is especially suited to measure the effects of different canopy species on understory composition. In such an area, the likelihood of factors other than overstory being a major cause of understory variation is small.

### Methods

Ten individuals of each of three tree and one shrub species (i.e., ponderosa pine, Rocky Mountain juniper, Gambel oak, and snowbrush ceanothus) were chosen for the study. Eight quadrats (0.25 $m^2$) were placed around each individual tree or shrub. Four of these quadrats were placed inside the cylinder of the canopy (i.e., in the area of litter deposition), and four were placed outside the influence of the canopy (2 m beyond the outside of the canopy cylinder). To eliminate bias, quadrats were consistently placed one at each direction of the compass. Quadrats were subdivided into four equal units of .0625 $m^2$ each.

Sample trees or shrubs were chosen at random within the study area and were marked for relocation. Quadrat sites, after selection, were also marked for aid in relocation. Presence or absence of individual plant species in the understory was determined for all four subunits of each quadrat.

All species rooted in the quadrat were recorded. Frequency of each plant species was determined by dividing the number of quadrat subdivisions in which a species occurred by the number of subdivisions sampled. Percent presence for all species encountered was computed as the total number of quadrats in which a species occurred

divided by the total number of quadrats examined (Curtis and McIntosh, 1951). Total living plant cover and composition of plant cover by lifeform was measured at each quadrat using an ocular estimate method (Daubenmire, 1959).

Light intensity was measured in foot-candles at each quadrat, and averages were computed for the understory and open-area quadrats associated with each canopy species. The data were collected in July 1975. All readings were taken between the hours of 12:00 noon and 2:00 p.m. on cloud-free days, the last two days of the study.

Soil pH was measured by the colorimetric method in the field to avoid pH changes which can occur when soil is stored moist.

Litter depth was measured at the center of all quadrats taken, and soil depth was determined by the average of five penetrometer readings in each quadrat (one at each corner and one in the center).

Data were analyzed by stepwise discriminant analysis (Klecka, 1975). The conclusions of the discriminant analysis were supported by similarity indices (Ruzicka, 1958), cluster analysis (Sneath and Sokal, 1973), correlation analysis and chi-squared contingency table analysis (Steel and Torrie, 1960).

Plant identifications follow Welsh and Moore (1973).

#### Results and Discussion

Characteristics of the environment and the vegetation types associated with understory and open-area communities are summarized in Table 1 for the four canopy species. As expected, light intensity values are consistently lower for the understory communities. Understory communities have consistently higher pH (more basic), except for ponderosa pine which shows an understory tending to be slightly more acidic than the open area. Both litter depth and soil depth are far greater in the understory communities than outside the canopies. Litter cover is much greater in the understory, while cover of

TABLE 1. Average measured values of environmental and vegetation parameters for understory and open area communities.

| | **Pinus ponderosa** | | **Ceanothus velutinus** | | **Juniperus scopulorum** | | **Quercus gambelii** | |
|---|---|---|---|---|---|---|---|---|
| | understory | open area | understory | open area | understory | open area | understory | open area |
| Light intensity (foot candles) | 117 | 225 | 123 | 339 | 168 | 295 | 76 | 242 |
| Soil pH | 6.3 | 6.4 | 6.6 | 6.4 | 7.4 | 6.4 | 6.6 | 6.4 |
| Litter depth (cm) | 6.0 | 0.6 | 2.1 | 0.1 | 2.5 | 0.3 | 2.3 | 0.2 |
| Soil depth (cm) | 10.5 | 5.3 | 6.7 | 4.4 | 6.1 | 4.0 | 8.5 | 5.7 |
| % Living cover* | 17.6 | 29.8 | 17.9 | 37.7 | 32.2 | 44.4 | 23.8 | 33.1 |
| % Litter cover* | 72.9 | 39.9 | 60.2 | 18.1 | 52.0 | 18.7 | 63.1 | 27.1 |
| % Exposed rock* | 9.5 | 30.3 | 21.9 | 52.2 | 15.8 | 36.9 | 13.1 | 39.5 |
| % Shrubs | 26.8 | 27.1 | 37.0 + | 23.9 | 48.0 | 22.9 | 27.7 | 18.4 |
| % Perennial Forbs | 5.2 | 11.4 | 18.9 | 36.5 | 8.0 | 31.2 | 15.6 | 27.4 |
| % Perennial grasses | 11.5 | 4.0 | 13.9 | 7.1 | 16.9 | 10.4 | 22.8 | 14.0 |
| % Annuals | 56.6 | 57.5 | 30.2 | 32.4 | 27.1 | 35.6 | 32.9 | 40.2 |
| Average number of species/tree | 10.5 | 11.9 | 14.2 | 14.9 | 10.9 | 14.3 | 12.7 | 14.0 |
| Average number of species/quadrat/tree | 4.6 | 6.2 | 7.1 | 6.9 | 5.4 | 6.3 | 7.4 | 8.4 |

*These three values are normalized so they sum to 100%.

+This figure does not include the cover of the overstory shrub, **Ceanothus velutinus.**

exposed rock is greater in the open-area communities. Living cover is higher in the open-area communities except for oak.

Species preferences for understory and open areas were obtained by taking the difference of total species frequencies in canopy-covered and open stands and normalizing by dividing by the total species frequency in all stands (Table 2). The resulting index runs from –1 to 1. Those species with the highest positive values were found most often under the canopy while those species with the greatest negative values were found most often in open areas. The relationship of specific understory species to these canopy species has been studied and reported elsewhere (Evenson *et al.*, 1980).

In order to clarify relationships of vegetation types and environmental factors, discriminant analysis (Klecka, 1975) was applied to the understory and open-area stands in several combinations.

The first analysis was based on percent cover by lifeform for all stands and utilized four categories of lifeform: shrubs, perennial forbs, perennial grasses, and annuals. This analysis correctly classified 79 percent of the stands (Table 3.A), and the presence of forbs was the most important factor in the separation. A second analysis based on

TABLE 2. Species preference list for understory and open-area community types. Life-form codes are e = evergreen, sh = shrub (so esh = evergreen shrub), f = forb, g = grass, c = cool-season or spring ephemeral but perennial, a = annual, t = tree.

| Species | Lifeform | Index |
|---|---|---|
| **Understory Preference** | | |
| Antennaria luzuloides | f | 1.00 |
| Arctostaphylos uva-ursi | esh | 1.00 |
| Chenopodium ambrosioides | a | 1.00 |
| Euphorbia robusta | f | 1.00 |
| Juniperus communis | esh | 1.00 |
| Melica bulbosa | g | 1.00 |
| Pinus contorta | et | 1.00 |
| Purshia tridentata | sh | 1.00 |
| Quercus gambelii | t | 1.00 |
| Thalictrum fendleri | f | 1.00 |
| Agropyron trachycaulum | g | .56 |
| Prunus virginiana | sh | .54 |
| Viola purpurea | f | .52 |
| Stellaria jamesiana | cf | .51 |
| Achillea millefolium | f | .43 |
| Carex geyeri | eg | .36 |
| Silene menziesii | ef | .33 |
| Bromus ciliatus | g | .32 |
| Carex rossii | eg | .31 |
| Tragopogon dubius | a | .25 |
| **No Apparent Preference** | | |
| Rosa woodsii | sh | .20 |
| Symphoricarpos oreophilus | sh | .20 |
| Pachystima myrsinites | esh | .19 |
| Poa pratensis | g | .11 |
| Agropyron subsecundum | g | .09 |
| Ceanothus velutinus | esh | .09 |
| Stipa lettermanii | g | .09 |
| Mahonia repens | esh | .08 |
| Comandra umbellata | ef | .07 |
| Eriogonum heracleoides | esh | .07 |
| Solidago multiradiata | f | .05 |
| Agropyron spicatum | g | 0.00 |
| Pinus ponderosa | et | 0.00 |
| Taraxacum officinale | f | 0.00 |
| Viguiera multiflora | f | 0.00 |
| Viola nuttallii | cf | 0.00 |
| Hydrophyllum capitatum | cf | -.02 |
| Lomatium grayi | f | -.05 |
| Potentilla glandulosa | f | -.11 |
| Collinsia parviflora | a | -.13 |
| Collomia linearis | a | -.19 |
| Thlaspi montanum | f | -.20 |
| **Open-area Preference** | | |
| Aster chilensis var. adsc. | f | -.28 |
| Allium acuminatum | cf | -.30 |
| Agoseris glauca | f | -.31 |
| Chenopodium fremontii | a | -.32 |
| Cirsium undulatum | f | -.33 |
| Poa curta | g | -.36 |
| Sedum stenopetalum | f | -.36 |
| Crypantha circumscissa | a | -.42 |
| Amelanchier alnifolia | sh | -.50 |
| Polygonum douglasii | a | -.51 |
| Solidago sparsiflora | f | -.53 |
| Apocynum androsaemifolium | f | -.78 |
| Chrysopsis villosa | f | -.79 |
| Gayophytum ramosissimum | a | -.91 |
| Antennaria rosea | f | -1.00 |
| Artemisia tridentata | esh | -1.00 |
| Bromus tectorum | g | -1.00 |
| Erysimum asperum | f | -1.00 |
| Galium boreale | f | -1.00 |
| Ipompsis aggregata | f | -1.00 |
| Mertensia brevistyla | f | -1.00 |
| Osmorhiza obtusa | f | -1.00 |
| Penstemon sp. | f | -1.00 |
| Poa fendleriana | g | -1.00 |
| Stipa columbiana | g | -1.00 |

TABLE 3. Discriminant analysis summaries.

A. Separation of understory and open-area stands based on lifeform data.

| | F to Enter or Remove | Wilk's Lambda | Significance |
|---|---|---|---|
| 1. % forbs | 21.453 | .784 | .001 |
| 2. % grasses | 13.361 | .668 | .001 |
| 3. % shrubs | 3.870 | .636 | .001 |

B. Separation of understory and open-area stands based on environmental data.

| | F to Enter or Remove | Wilk's Lambda | Significance |
|---|---|---|---|
| 1. litter cover | 118.294 | .397 | .001 |
| 2. soil pH | 18.342 | .321 | .001 |
| 3. light intensity | 13.990 | .271 | .001 |
| 4. litter depth | 11.678 | .235 | .001 |
| 5. soil depth | 2.449 | .227 | .001 |
| 6. % exposed rock | 1.151 | .223 | .001 |

C. Classification of understory stands into community types based on lifeform and cover data.

| | F to Enter or Remove | Wilk's Lambda | Significance |
|---|---|---|---|
| 1. % annuals | 6.605 | .645 | .001 |
| 2. % forbs | 6.152 | .422 | .001 |
| 3. % grasses | 2.106 | .277 | .001 |
| 4. % cover | 2.106 | .277 | .001 |
| 5. % shrubs | 1.525 | .242 | .001 |

D. Classification of understory stands into community types based on tree-influenced environmental variables.

| | F to Enter or Remove | Wilk's Lambda | Significance |
|---|---|---|---|
| 1. litter cover | 23.109 | .342 | .001 |
| 2. soil pH | 18.388 | .133 | .001 |
| 3. litter depth | 8.863 | .074 | .001 |
| 4. light intensity | 3.954 | .055 | .001 |

the environmental parameters, litter depth, soil depth, percent exposed rock, light intensity, litter cover, and soil pH correctly classified 99 percent of the stands into understory and open-area community types. Litter cover, soil pH, light intensity, and litter depth were the factors most responsible for the separation (Table 3.B).

These analyses indicate that there are significant differences between understory and open-area plant communities both in vegetation type and in physical environment. The lifeforms most affected by differences in environment were perennial forbs, perennial grasses and shrubs.

Discriminant analysis was employed further in five separate analyses to determine which environmental factors and which lifeform types varied significantly between the understories of different canopy species. The first analysis (Table 3.C) was based on lifeform and total living cover. Seventy percent of the understory stands were correctly classified; annuals were the most powerful discriminating factor. An analysis based on lifeform type only showed slightly decreased capacity for resolution, with only 68 percent of the stands classified correctly.

The first of three analyses based on environmental factors considered tree-influenced parameters: litter depth, litter cover, soil pH, and light intensity (Table 3.D). This analysis correctly grouped 93 percent of the stands with litter cover the most im-

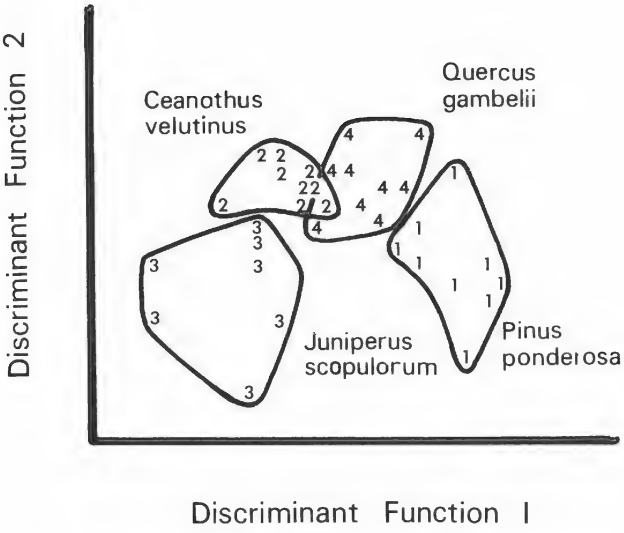


Figure 1. Discriminant analysis of understory stands based on tree-influenced environmental factors.

portant discriminator (Fig. 1). A second analysis added soil depth and percent exposed rock to the above factors. The result was exactly the same as in the previous analysis, with 93 percent of the stands classified correctly. The last analysis considered only soil depth and percent exposed rock. Fifty-five percent of the stands were classified correctly based on these two factors alone.

These analyses show that there are significant differences in the lifeform types under the canopies of different overstory species. Canopy-influenced factors are primarily responsible for differences in habitat between the understories.

The above results of discriminant analysis were supported by other analyses. Similarity indices indicated that the open areas were more uniform in species composition than the understories. Open-area stands showed a mean similarity among themselves of 53 percent (Ruzicka similarity index); understory stands showed a mean of 44 percent. The lower average similarity in the understory stands is consistent with the hypothesis that the tree species influence their understory communities in different ways.

Cluster analysis was performed on all stands in order to examine the separation of understory and open-area communities. In addition, understory stands were clustered in order to study the separation of understory communities according to the associated canopy species. Results again supported the conclusions of the above analyses. Eighty percent of open-area stands were grouped into the same cluster on the basis of species composition; at the same time, 80 percent of understory stands fell into a second major category. Clustering was also performed using environmental data. Again, open-area stands fell into groups which were strongly independent of understory stands: 89 percent of the stands were classified with their own kind. Clustering according to lifeform gave inconclusive results.

Cluster analysis of understory stands on the basis of environmental data classified 73 percent of the stands correctly with respect to the associated canopy tree species. Furthermore, the oak understory stands were separated from evergreen understories. Cluster of the understory stands by lifeform types was suggestive but not conclusive as regards differences associated with canopy species.

Correlation analysis was done on data from all stands to determine how lifeform types correlate with environmental factors as well as with each other. Results were generally in agreement with relationships determined from other analyses.

Finally, species were classified by lifeform type, as in Table 2, according to their occurrence in understory or open-area sample units. A contingency table of four rows (shrubs, forbs, grasses, annuals) and two columns (understory vs. open-area occurrence) was constructed, and $X^2$ was calculated to test independence of the two classification variables. The hypothesis of independence was rejected ($p < 0.001$), which supports the conclusions of the above analyses. Shrubs and grasses are more common in understory communities; in contrast, forbs and annuals are more common in open environments. The pattern suggests a moisture relationship since throughfall precipitation is reduced by the tree canopy and thickness of litter (Anderson *et al.*, 1969), and shrubs and grasses are generally considered to be more xeric than forbs (Jaynes and Harper, 1978). (In our view, homogeneity of soils in the study area minimizes the role of soil texture in these relationships.)

Other literature indicates that mineral nutrients are more concentrated in canopy-covered soils than in adjacent open areas (Zinke, 1962; Tiedemann and Klemmedson, 1973; Greenwood and Brotherson, 1978; Barth and Klemmedson, 1978). Such improved nutrient conditions, coupled with higher availability of nutrients (Tiedemann and Klemmedson, 1973) have also been shown to parallel increased abundance and growth of grasses in canopy-covered habitats (Humphrey, 1962; Tiedemann, 1970; Barth and Klemmedson, 1978). Also, annuals, which were more common in our open-area communities, are more efficient in nutrient uptake (Rice, Penfound, and Rohrbaugh, 1963; Roux and Warren, 1963), and thus should be better adapted to less fertile open-area sites.

A similar contingency table analysis was carried out by classifying species in Table 2 as evergreen or nonevergreen. Evergreen species were more common in understory habitats and nonevergreen species in open-area habitats (significant at $p < 0.001$).

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# Food Habits of Seven Species of Lizards from Malheur County, Southeastern Oregon

**Abstract**

Food habits of 110 lizards of 7 species are examined and related to habitat in the high desert rangelands of southeastern Oregon. The lizards include: 11 collared lizards (*Crotaphytus collaris*), 21 leopard lizards (*Crotaphytus wislizeni*), 24 western whiptails (*Cnemidophorus tigris*), 39 western fence lizards (*Sceloporus occidentalis*), 8 side-blotched lizards (*Uta stansburiana*), 5 desert horned lizards (*Phrynosoma platyrhinos*), and 2 short-horned lizards (*Phrynosoma douglassi*).

## Introduction

Relatively little information exists on foods of lizards (Oliver, 1955; Otvos, 1977; Simon, 1976) and none on foods of lizards in Oregon. The purpose of this paper is to present such information and to examine the degree of food and habitat resource partitioning, if any, among species.

## Methods and Materials

Lizards were collected over a 3-year period (1975-1977) from May through September by hand and by shooting with a .22 caliber rifle and shot cartridges. Carcasses were frozen and returned to the laboratory for dissection. Stomach contents were preserved in 10 percent formalin. Food items were identified; volume percentages of each food in each stomach were visually estimated using a 10 to 70 power zoom dissection microscope.

## Description of Study Area

The study area was located in the dominant shrub-steppe communities of the Owyhee Upland Province in southeastern Oregon (Franklin and Dyrness, 1973). Plant communities referred to in this study have been discussed by and names follow Dealy *et al.*, 1981).

## Results and Discussion

Foods eaten by the seven species of lizards are detailed in Table 1, and summarized by Order in Table 2.

TABLE 1. Foods of seven species of lizards from Oregon.

| | **Sceloporus occidentalis** | | **Cnemidophorus tigris** | | **Crotaphytus wislizeni** | | **Crotaphytus collaris** | | **Uta stansburiana** | | **Phrynosoma platyrhinos** | | **Phrynosoma douglassi** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| n = | 39 | | 24 | | 21 | | 11 | | 8 | | 5 | | 2 | |
| | % | | % | | % | | % | | % | | % | | % | |
| | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq |
| Orthoptera | | | | | | | | | | | | | | |
| Acridiae | 41.3 | 53.8 | 19.0 | 33.3 | 39.8 | 61.9 | 53.2 | 81.8 | 31.3 | 50.0 | | | | |
| Gryllidae | 10.8 | 20.5 | 0.6 | 4.2 | 6.4 | 9.5 | 5.9 | 18.2 | | | | | | |
| Unidentified | | | 7.5 | 8.3 | | | | | | | | | | |
| Hymenoptera | | | | | | | | | | | | | | |
| Andrenidae | | | | | | | 1.4 | 9.1 | | | | | | |
| Apoidea | 5.0 | 10.6 | | | 9.3 | 33.3 | | | | | | | | |
| Chrysididae | 0.4 | 7.7 | | | 0.7 | 4.8 | 1.4 | 18.2 | | | | | 2.5 | 50.0 |
| Formicidae | 2.7 | 30.8 | 1.8 | 20.8 | 1.4 | 14.3 | 1.4 | 18.2 | 3.8 | 12.5 | 89.4 | 100 | 93.0 | 10.0 |
| Sphecidae | 2.1 | 5.1 | | | | | | | | | | | | |
| Vespidae | | | | | 3.6 | 4.8 | 1.4 | 9.1 | | | | | | |
| Unidentified | 0.4 | 2.6 | | | | | | | | | | | | |
| Coleoptera | | | | | | | | | | | | | | |
| Carabidae | 3.7 | 10.3 | 4.4 | 8.3 | 1.7 | 4.8 | | | 3.8 | 12.5 | 0.4 | 20.0 | | |
| Cerambycidae | | | | | 1.4 | 4.8 | | | | | | | | |
| Cleridae | 0.4 | 2.6 | | | | | | | | | | | | |
| Curculionidae | | | 1.3 | 4.2 | | | | | | | | | | |
| Elateridae | 1.3 | 2.6 | | | | | | | | | | | | |
| Histeridae | 0.3 | 2.6 | | | | | | | | | 1.6 | 20.0 | | |
| Melyridae | 0.4 | 5.1 | | | | | | | | | | | | |
| Nitidulidae | | | 1.9 | 4.2 | | | | | | | | | | |
| Scarabaeidae | 1.1 | 12.8 | 0.2 | 4.2 | 1.4 | 9.5 | | | | | | | | |
| Staphylinidae | 0.5 | 2.6 | | | | | | | 1.9 | 12.5 | | | | |
| Tenebrionidae-adult | 8.7 | 33.3 | 2.1 | 12.5 | 7.4 | 14.3 | 2.7 | 18.2 | | | 6.4 | 60.0 | 2.0 | 50.0 |
| Tenebrionidae-larva | | | 1.7 | 4.2 | | | | | | | | | | |
| Unident. Larvae | | | | | | | 0.5 | 9.1 | | | 0.6 | 20.0 | | |
| Unident. Adult | 1.7 | 7.7 | 0.04 | 4.2 | 0.4 | 4.8 | 2.7 | 9.1 | | | | | 1.0 | 50.0 |
| Hemiptera | | | | | | | | | | | | | | |
| Anthocoridae | | | | | | | | | 0.6 | 12.5 | | | | |
| Lygaeidae | 0.1 | 2.6 | | | | | 0.5 | 9.1 | 6.3 | 25.0 | | | | |
| Pentatomidae | 1.0 | 2.6 | 5.6 | 8.3 | | | 4.5 | 27.3 | | | | | | |
| Reduviidae | | | | | | | | | | | | | 1.5 | 50.0 |
| Unidentified | 0.9 | 7.7 | | | 5.2 | 14.3 | 5.2 | 18.2 | 13.1 | 25.0 | | | | |

TABLE 1. (Continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Homoptera | | | | | | | | | | | | |
| Cercopidae | | | | | | | | | 1.9 | 12.5 | | |
| Cicadellidae | 0.1 | 2.6 | | | | | | | | | | |
| Fulgoridae | | | 0.8 | 4.2 | | | | | | | | |
| Cicadidae | | | 7.1 | 12.5 | 5.2 | 4.8 | 2.7 | 9.1 | | | | |
| Diptera | | | | | | | | | | | | |
| Asilidae | | | | | 1.7 | 9.5 | | | | | | |
| Muscoidea | 0.5 | 2.6 | | | 1.7 | 9.5 | | | | | | |
| Otitidae | | | | | | | 0.5 | 9.1 | | | | |
| Scarophagidae | | | | | 1.2 | 4.8 | | | | | | |
| Unidentified | | | | | | | | | 3.8 | 12.5 | | |
| Lepidoptera | | | | | | | | | | | | |
| Adult | 2.2 | 5.1 | 11.9 | 33.3 | | | 12.3 | 36.4 | | | | |
| Larvae | 3.3 | 12.8 | 16.9 | 37.5 | 3.1 | 19.0 | 1.4 | 9.1 | 14.4 | 25.0 | | |
| Neuroptera | | | | | | | | | | | | |
| Hemerobiidae | 0.1 | 2.6 | | | 0.8 | 4.8 | | | | | | |
| Myrmeleontidae | | | 0.6 | 4.2 | | | | | | | | |
| Unident. Adult | | | 0.6 | 4.2 | | | | | | | | |
| Unident. Larvae | | | 0.6 | 4.2 | | | | | | | | |
| Odonata (Damselfly) | 2.9 | 7.7 | | | 1.4 | 14.3 | | | | | | |
| Dermaptera | | | 0.2 | 4.2 | | | | | | | | |
| Unidentified Insect | | | | | | | | | | | | |
| Adult | 2.5 | 25.6 | 2.3 | 20.8 | | | 1.6 | 18.2 | 3.1 | 25.0 | 0.6 | 20.0 |
| Larvae | 2.9 | 7.7 | 0.2 | 4.2 | | | | | | | | |
| Araneida | 2.7 | 10.3 | 11.3 | 37.5 | 7.4 | 19.0 | | | 16.3 | 37.5 | 0.6 | 20.0 |
| Chilopoda | | | | | | | | | | | 0.4 | 20.0 |
| Pseudoscorpion | | | 0.2 | 4.2 | | | | | | | | |
| Phalangida | | | 0.2 | 4.2 | | | | | | | | |
| Vegetation | | | 0.8 | 8.3 | | | 0.9 | 9.1 | | | | |
| | 100.0 | | 99.8 | | 99.5 | | 100.2 | | 100.3 | | 100.0 | 100.0 |

TABLE 2. Summary of major foods of seven species of lizards from Oregon in percent volume by order of prey species.

| | n | Orthoptera | Coleoptera | Hymenoptera | Hemiptera | Homoptera | Lepidoptera | Araneida |
|---|---|---|---|---|---|---|---|---|
| **Sceloporus occidentalis** | 39 | 52.1 | 18.1 | 10.6 | 2.0 | 0.1 | 5.5 | 2.7 |
| **Cnemidophorus tigris** | 24 | 27.1 | 11.6 | 1.8 | 5.6 | 7.9 | 28.8 | 11.3 |
| **Crotaphytus wislizeni** | 21 | 46.2 | 12.3 | 15.0 | 5.2 | 5.2 | 3.1 | 7.4 |
| **Crotaphytus collaris** | 11 | 56.1 | 5.9 | 4.4 | 10.2 | 2.7 | 13.7 | — |
| **Uta stansburiana** | 8 | 31.3 | 5.7 | 3.8 | 20.0 | 1.9 | 14.4 | 16.3 |
| **Phrynosoma platyrhinos** | 5 | — | 9.0 | 89.4 | — | — | — | 0.6 |
| **Phrynosoma douglassi** | 2 | — | 3.0 | 95.5 | 1.5 | — | — | — |

### Specific Habitat and Food Considerations

Western fence lizards (*Sceloporus occidentalis*), the most adaptable Oregon lizards, occupy a wide range of habitats (Clark, 1973; Davis and Verbeek, 1972; Rose, 1976; Stebbins, 1966). In southeastern Oregon, they were associated with a variety of man-made habitats, such as homesteads, rock walls, rock jacks, and rock cribs; and geomorphic habitats, such as cliffs, talus, and lava flows (Maser *et al.*, 1979a,b). The major habitat component for western fence lizards was igneous rock, such as rhyolite and basalt, with crevices into which the lizards could move at will. The major foods of these lizards were orthopterans (52.1 percent) and coleopterans (18.1 percent) by volume.

Western whiptails (*Cnemidophorus tigris*) inhabited a variety of plant communities in southeastern Oregon, such as Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)/bunchgrass, black greasewood (*Sarcobatus vermiculatus*)/grass, and shadscale saltbrush (*Atriplex confertifolia*)/bunchgrass. The soils must be friable, however, or these lizards cannot inhabit an area (Burt, 1931; Maser, unpubl. data; Pianka, 1970). Major foods of western whiptails were lepidopterans (28.8 percent) and orthopterans (27.1 percent) by volume.

Leopard lizards (*Crotaphytus wislizeni*) were widly distributed in southeastern Oregon. Although they may have been sympatric with western whiptails in shrub communities, such as Wyoming big sagebrush/bunchgrass, black greasewood/grass, or shadscale saltbrush/bunchgrass, leopard lizards tended to occupy areas of sparser herbaceous vegetation than did whiptails. Leopard lizards therefore often concentrated along edges of roads where soils were friable and where they had ample running room (Maser, unpubl. data; Storm, 1966). Major foods of leopard lizards were orthopterans (46.5 percent) and hymenopterans (15.0 percent) by volume.

Collared lizards (*Crotaphytus collaris*) inhabit talus in areas of low, sparse vegetation. Talus is their main habitat component (Fitch, 1956; Maser *et al.*, 1979a; Stebbins, 1966; Storm, 1966). Because of the sparse distribution of this habitat in southeastern Oregon, the distribution of collared lizards was limited to widely scattered colonies. Major foods were orthopterans (59.1 percent) and lepidopterans (13.7 percent) by volume.

Side-blotched lizards (*Uta stansburiana*) occur generally throughout central and eastern Oregon (Nussbaum and Diller, 1976); but they were uncommon in southeastern Oregon during this study. Associated with rocky habitats in most of central and eastern Oregon, side-blotched lizards in our study area were also found in the

shadscale saltbrush/bunchgrass community in the total absence of rocky areas. Tinkle (1967) and Davis and Verbeek (1972) also observed these lizards in habitats without rocky areas in some parts of their range. Major foods of the side-blotched lizard were orthopterans (31.3 percent), araneidans (16.3 percent), and lepidopterans (14.4 percent) by volume.

Desert horned lizards (*Phrynosoma platyrhinos*), a widely distributed species (Pianka and Parker, 1975; Tanner and Krogh, 1973), were nowhere abundant in southeastern Oregon. Major foods of the desert horned lizard were hymenopterans, primarily formicids (89.4 percent) and coleopterans (9.0 percent) by volume.

Short-horned lizards (*Phrynosoma douglassi*) are much more widely distributed in Oregon than are desert horned lizards (Stebbins, 1966; Storm, 1966). Locally abundant in central Oregon where the soil is sandy, they were seldom encountered within our study area. Major foods of the short-horned lizards also were hymenopterans (95.5 percent), mostly formicids (93.0 percent), with coleopterans (3.0 percent) by volume.

### Comparative Habitat and Food Considerations

Both species of horned lizards fed primarily on formicids, including the western harvester ant (*Pogonomyrmex occidentalis*), which concurs with Clark and Comanor (1976) and Tanner and Krogh (1973). Other species identified as food items during our study included the following: *Pogonomyrmex californicus, Myrmecophagus mimicus, Crematogaster coarctata vermiculata, Camponotus* sp., and *Lasius* sp. Pianka and Parker (1975) found formicids (56.61 percent) and coleopterans (22.28 percent), by volume, to be the major foods of 236 desert horned lizards; but orthopterans (40.6 percent), coleopterans (34.7 percent), and formicids (15.1 percent), by volume, were the main food items in the 21 short-horned lizards that they examined. Our small sample size of horned lizards precludes much speculation, but since the other five species of lizards in our study area ate ants only in small amounts (Table 1), a certain amount of food resource partitioning did occur.

Food relationships among the other five species of lizards, illustrated by the following list of prey items by order consisting of 10 percent or more of the stomach volume, were:

*Sceloporus occidentalis*—Orthoptera-Coleoptera-Hymenoptera
*Cnemidophorus tigris*—Lepidoptera-Orthoptera-Coleoptera-Araneida
*Crotaphytus wislizeni*—Orthoptera-Hymenoptera-Coleoptera
*Crotaphytus collaris*—Orthoptera-Lepidoptera-Hemiptera
*Uta stansburiana*—Orthoptera-Hemiptera-Araneida-Lepidoptera

There obviously was considerable overlap in the diets of the five species of lizards. For example, orthopterans, particularly grasshoppers, figured prominently in the diets of these lizards; this finding is not surprising because grasshoppers were exceedingly abundant in all habitats during the study. Coleopterans and lepidopterans were also abundant, widely distributed, and were major food items used by three of the five lizard species.

There were, however, some habitat-related differences that, along with differences in food habits, can be viewed as resource partitioning. For example, western fence lizards and collared lizards occasionally occurred together, and both required rocks as a habitat

component; but fence lizards did most of their feeding on the rocks, whereas collared lizards did most of their feeding on the ground. So except for use of the ubiquitous grasshoppers, their major foods differed. The fence lizards concentrated on coleopterans (18.1 percent) and hymenopterans (10.6 percent) by volume; collared lizards concentrated on lepidopterans (13.7 percent) and hemipterans (10.2 percent) by volume.

Where collared lizards and leopard lizards (both ground predators) were sympatric, their diets differed in that the leopard lizards ate primarily hymenopterans (15.0 percent) and coleopterans (12.3 percent) by volume. Again, where fence lizards were also sympatric with collared and leopard lizards, they fed mainly on whatever alighted on the rocks.

Western whiptails were most abundant in the black greasewood/grass community where they fed under the greasewood plants, which accounts for the dominance of lepidopterans (28.8 percent by volume) and araneidans (11.3 percent by volume) in their diet. Although collared lizards also had a high percent of lepidopterans (13.7 percent by volume) in their diet, they fed mostly on adults (12.3 percent by volume), whereas whiptails ate primarly larvae (16.9 percent by volume). Collared lizards did not eat araneidans as did western whiptails.

Lepidopterans and araneidans were not major dietary items of leopard lizards (3.1 percent and 7.4 percent by volume, respectively). Hymenopterans, on the other hand, were an important dietary item for leopard lizards (15.0 percent by volume) as opposed to 1.8 percent by volume for whiptails. In addition, whiptails had a more catholic diet than did either the collared lizard or the leopard lizard.

Side-blotched lizards were the smallest of the five species. They concentrated on hemipterans (20.0 percent by volume) and araneidans (16.3 percent by volume). Although some interspecific competition for food may have existed between adult side-blotched lizards and the young of western fence lizards, collared lizards, leopard lizards, and whiptails, there were enough differences in microhabitat and prey selection to allow a certain amount of sympatry. Further, side-blotched lizards were more restricted in their diet than were the other four species. Such selectivity may be related to the small size of adult individuals, preference for certain prey types, or both, but we assume it was partly related to the small sample size.

#### Conclusions

There was considerable resource overlap, both in food and habitat, among the seven species of lizards studied. When food habits and habitat use were viewed independently, a clear picture of resource partitioning did not emerge. For example, a rank order correlation coefficient was calculated between sample size and number of the most common order (Orthoptera) from data in Table 2. The correlation ($r = 0.67$) is significant ($P < .05$), and indicates that variation in the abundance of Orthoptera may be caused by variation in sample size.

When food habits and habitat use were viewed simultaneously some resource partitioning became apparent, but it also became obvious that, to demonstrate resource partitioning clearly, sample sizes for food habit analyses should be considerably larger per species.

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# Nesting Populations and Breeding Chronologies of Gulls, Terns, and Herons on the Upper Columbia River, Oregon and Washington

## Abstract

Colonial nesting Great Blue Herons (*Ardea herodias*), Black-crowned Night Herons (*Nycticorax nycticorax*), California and Ring-billed Gulls (*Larus californicus* and *L. delawarensis*), and Caspian and Forster's Terns (*Sterna caspia* and *S. forsteri*) were studied during 1977 and 1978 on the Columbia River between Portland, Oregon, and Priest Rapids, Washington. Numbers of nests at the 17 known colonies were counted or estimated each year; temporal limits were established for egg-laying, incubation, hatching, young in colony, and fledging of each species during 1978.

Both gull species nested in about equal proportions, numbering in excess of 16,000 breeding pairs in 1978. Great Blue Heron colonies generally were small and scattered, totaling slightly more than 300 nests. About 90 to 100 pairs of Black-crowned Night Herons nested at the two known colonies in the study area. Caspian and Forster's Terns totaled slightly more than 200 and 400 breeding pairs, respectively.

Egg-laying through fledging occurred between late April and late August for gulls and terns, but this period was prolonged from February or March through August for both herons. These differences in chronologies were attributed to greater intercolony synchrony displayed by gulls and terns. Chronological differences require that herons be counted twice during the nesting season to enumerate breeding pairs accurately, whereas accurate counts of gulls and terns may be obtained during a single count in May. Active nests of gulls and terns occur near reservoir levels for extended periods, a factor that should be considered in planning water regulation regimes.

## Introduction

Future use of hydroelectric power dams on the Columbia River to meet peak power demands will involve operational modifications that increase the frequency and magnitude of reservoir fluctuations within present operating limits (U.S. Army Corps of Engineers, 1977). These changes in fluctuation regimes would adversely affect certain bird species if nest sites or feeding areas were altered during critical periods. Colonial nesting gulls, terns, and herons comprise an important avian group breeding close to water along the Columbia River. Aside from information on gulls presented by Broadbooks (1961) and Hanson (1963) and on Great Blue Herons by Nehls (1972) and Henny and Kurtz (1978), few data exist concerning the breeding status of colonial nesters in this area.

This study was conducted to ascertain nesting populations and breeding chronologies of gulls, terns, and herons nesting in a major part of the Columbia River. These data were collected to quantify reproductive potential and to delineate time periods during which nests and young are vulnerable to water fluctuations and other

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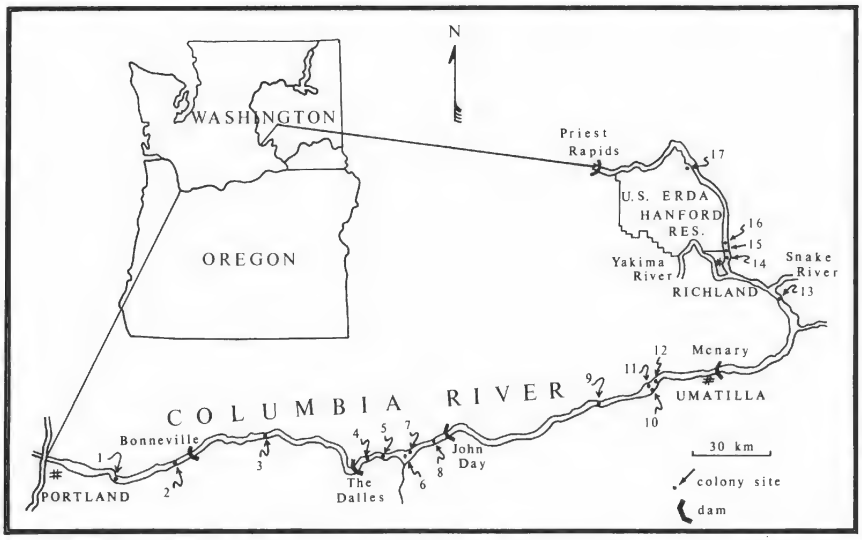


Figure 1. Columbia River study area and location of colony sites used by gulls, terns, and herons.

environmental perturbations. Furthermore, this paper provides data for comparison with population trend information to be collected in the future.

**Study Area**

The study area comprised 467 km of the Columbia River between Portland, Oregon, and Priest Rapids, Washington. This part of the river, largely impounded by lock and dam facilities, includes Bonneville, The Dalles, John Day, and McNary reservoirs as well as free-flowing areas below Bonneville dam and between Priest Rapids dam and Richland, Washington (Hanford Reach) (Fig. 1). Most of this area is located in the Columbia Basin physiographic province (Fenneman, 1931), characterized by a xeric climate with about 9 to 12° C average annual temperatures and 20 to 45 cm annual precipitation occurring primarily as rain from October through March (Natl. Ocean. Atmos. Admin. 1977-1978 a, b). Prevailing winds are westerly, reaching speeds to 55 kph along the river during summer months. The westernmost 120 km of the study area is in the Cascade provinces, characterized by slightly higher temperatures and a more mesic climate with 60 to 160 cm annual precipitation.

All except one colony site were located on islands, and those colonies selected for intensive study were in the xeric reach upstream from The Dalles (Fig. 1). Colony sites had slight relief (2 to 7 m) and were on sand/cobble or basalt substrates. Basalt sites were largely devoid of vegetation except where wind- and water-deposited soil supported small willows (*Salix* spp.) and mixed herbaceous species. Sand/cobble sites generally contained pepperweed (*Lepidium latifolium*) and horseweed (*Conyza canadensis*) on low, moist areas, grading to sand dock (*Rumex venosus*), lupine (*Lupinus* spp.), and buckwheat (*Eriogonum* spp.) on drier sites and sagebrush (*Artemisia* spp.) on the upland. Most islands were fringed with scattered Great Plains or black cottonwood (*Populus deltoides* and *P. trichocarpa*), willow, or mulberry

(*Morus alba*) from 3- to 15-m tall. The White Bluffs colony (#17) consisted of a stand of cottonwood about 100 m from the river. Franklin and Dyrness (1973) provided a detailed description of vegetation communities in this area.

#### Methods

Breeding populations on most of the 17 colony sites (Fig. 1) were obtained by total counts of active nests as recommended by Nettleship (1976). Primary counts were made when the main breeding contingent was well advanced in nesting at each colony. Numbers of new nests observed during subsequent visits were added to the primary count. Most colonies were small enough and nests were conspicuous enough to eliminate problems in obtaining total counts. Total counts were conducted at gull colonies only once each year during late incubation/early hatching of the main breeding contingent. Additional sample counts were made on selected gull colonies to monitor progression of nesting in 1978. Total counts were conducted on colonies 1 through 13 both years (see exception below). Error for counts of colonies with less than 100 nests was considered nil, and error for larger colonies was estimated as less than 5 percent.

Counts of gulls at colony 9 in 1977 and at colonies 14 to 16 in both years were based on transect and quadrat samples comprising about 10 percent of each colony. Transects and quadrats were subjectively placed on representative areas of all substrates within each colony. Total counts were derived by extrapolating sample counts for each substrate to total area of that type as estimated from aerial photos. Accuracy of this method was considered to be plus or minus 10 percent.

Breeding chronologies were obtained in 1978 from data collected during on-site examinations of colony sites 4, 6, 7, 8, 9, 11, and 13 at irregular 1- to 3-week intervals from mid-March through mid-July. These sites represented all known nesting by Black-crowned Night Herons and Caspian Terns and 36.0, 17.2, and 8.4 percent of the estimated nesting attempts by gulls, Great Blue Herons, and Forster's Terns, respectively. All other colony sites except #15 were visited during 1978 to assess the progression of breeding relative to colonies in which chronological data were collected. Deviations from estimated phase limits were not observed in these colonies.

During each visit to colonies, nest contents for each species were examined, and number of eggs and/or young and age of nestlings were recorded. Preliminary work in these colonies in 1977 provided experience in locating nests and assigning ages to nestlings based on appearance and plumage development. All nests were not enumerated during visits; rather, nests were sought that represented the extremes of each reproductive phase (see below). No attempt was made to identify nests individually except in the smaller heron colonies. In the large colonies, data were collected during surveys throughout each colony to ensure adequate coverage of all nesting attempts.

The reproductive phases considered were egg-laying, incubation, hatching, young in colony, and fledging. When possible, earliest dates of arrival at colonies were recorded. Efforts were concentrated on establishing the limits of each phase; however, timing within each phase was estimated for both species of herons based on known nest histories. Generally, visits to colonies were timely enough to permit direct observation of the limits for each phase from raw data. However, where backdating and postdating were necessary, calculations were made using information on clutch size,

laying rates, incubation behavior, and nestling periods extracted from Bent (1921, 1926), Gross (1923), Behle and Goates (1957), Palmer (1962), Pratt (1970), Vermeer (1970), and Smith and Diem (1972). Phase limits reported herein for egg-laying, incubation, and hatching are considered accurate within two days. Young in colony and fledging periods are only accurate within five days as a result of inherent variation in these periods and the greater amount of postdating necessary to establish these dates. Ring-billed and California Gulls were grouped for data collection because these species mixed on some colonies and differentiation of nests was often difficult. Supplementary observations indicated that the chronologies of the two species were sufficiently coincident to permit grouping.

## Results

Gulls represented the greatest proportion of all species, numbering in excess of 16,000 breeding pairs in 1978 (Table 1). Both species of gulls were present in approximately equal numbers on the study area. Some Ring-billed and California Guli nest counts from 1977 were presented and discussed previously (Conover *et al.*, 1979),

TABLE 1. Locations and counts of active nests for colonial nesting gulls, terns, and herons at 17 colony sites on the upper Columbia River, 1977 and 1978.

| Colony site | | | | | | |
|---|---|---|---|---|---|---|
| | | Distance from | No. visits | | Nest count | |
| No. | Name | river mouth (km) | 1978 | Species[a] | 1977 | 1978 |
| 1 | Reed Island | 201.3 | 2 | GBH | 94 | 87 |
| 2 | Pierce Island | 228.0 | 2 | GBH | b | 53 |
| 3 | Wells Island | 269.5 | 3 | GBH | 16 | 24 |
| 4 | Little Memaloose I. | 314.4 | 6 | CG | 428[e] | 477 |
| 5 | Brown's Island | 318.0 | 1 | GBH | b | 2 |
| 6 | Miller Island | 330.5 | 5 | GBH | b | 6 |
| 7 | Miller Rocks | 332.6 | 6 | CG | 521[c,e] | 794 |
| | | | | RBG | 521[c,e] | 124 |
| 8 | Rufus Bar | 338.4 | 6 | FT | 26 | 37 |
| 9 | Threemile Canyon I. | 411.6 | 5 | CG | 4377[c,e] | 4460[c] |
| | | | | RBG | 4377[c,e] | 4460[c] |
| | | | | CT | 184 | 210 |
| | | | | BCNH | 26 | 31 |
| 10 | River Snags | 440.5 | 2 | GBH | 9 | 2 |
| 11 | Sand Dune West I. | 440.5 | 6 | GBH | 16 | 20 |
| 12 | Telegraph Island | 442.8 | 4 | GBH | 3 | 0 |
| 13 | Foundation Island | 518.6 | 11 | GBH | 71[c] | 30 |
| | | | | BCNH | 71[c] | 51 |
| 14 | Richland (Isl. 20)[d] | 548.2 | 2 | CG | 1800[e] | 2000 |
| | | | | RBG | 2355[e] | 2605 |
| | | | | FT | 126 | 126 |
| 15 | Island 19[d] | 552.2 | — | FT | 50 | 50 |
| 16 | Island 18[d] | 554.5 | 2 | CG | 2955[e] | 3283 |
| | | | | RBG | 2246[e] | 2496 |
| | | | | FT | 228 | 228 |
| 17 | White Bluffs | 596.2 | 1 | GBH | b | 92 |

[a]BCNH = Black-crowned Night Heron, CG = California Gull, CT = Caspian Tern, FT = Forster's Tern, GBH = Great Blue Heron, RBG = Ring-billed Gull.

[b]Colony not visited or not known in 1977.

[c]Nests not differentiated during counts.

[d]Data courtesy R. E. Fitzner, Battelle-Northwest, Richland, Washington.

[e]Data previously reported by Conover **et al.** (1979) but included here for a complete listing. Data presented here are correct; the previously published table contained errors for some colonies.

but have been included in Table 1 to provide a comprehensive listing for the colonial nesters in the study area. Great Blue Herons were most widely distributed in the study area, but colonies were small and nests totaled about 300 each year (Table 1). Night Herons were less common (90 to 100 nests) and much more restricted in distribution. Forster's and Caspian Tern nests totaled about 400 and 200, respectively; colony 9 represented the only colony of Caspian Terns on the upper Columbia (Table 1).

The reproductive periods for gulls and terns were relatively short; whereas both species of herons exhibited greatly extended phases throughout the breeding season (Fig. 2). All species were actively nesting by late April and reproductive efforts were largely complete by late August. Estimated peak hatching for all species occurred 2 to 4 weeks following the first hatch and was most pronounced for gulls and Caspian Terns (Table 2, Fig. 3, 4). Nesting by all species occurred about 10 days earlier in 1978 than in 1977, indicating some annual variation in breeding.

Gulls were highly synchronized among all colonies examined; the first young hatched 14 to 15 May in each colony. About 53 percent of the gull nests hatched from 15 to 31 May (Table 2) and peak hatching occurred between 25 May and 10 June. The egg-laying through hatching period for gulls was extended to late June primarily by Ring-billed Gulls that used peripheral areas, although some California Gulls nested that late also. Egg-laying through fledging of young gulls extended from mid-April through early August; however, colonies were occupied longer when the extended

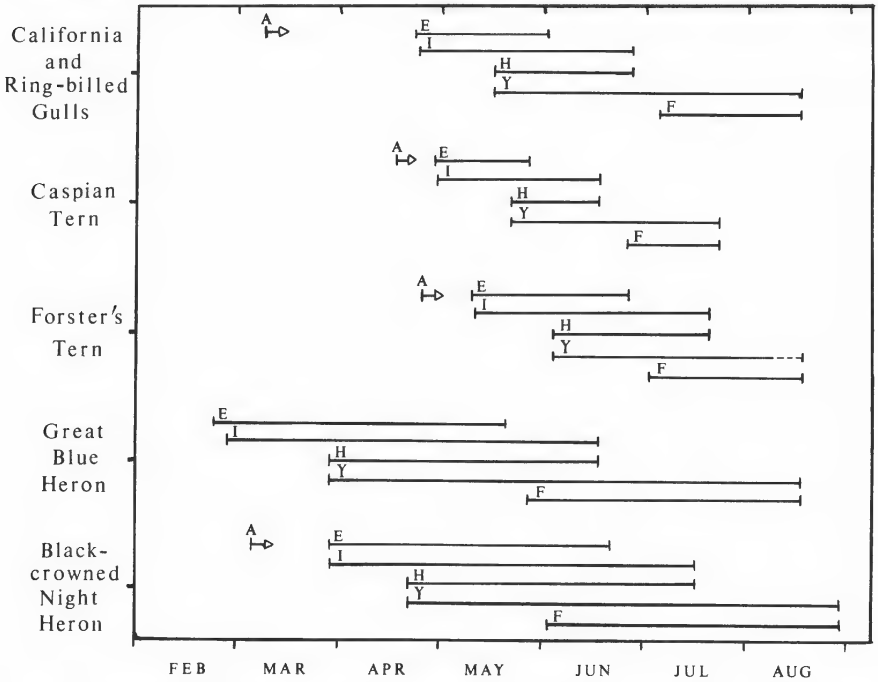


Figure 2. Breeding chronologies for colonial nesting gulls, terns, and herons on the upper Columbia River during 1978. A = Arrival at colony, E = Egg-laying, F = Fledging, H = Hatching, I = Incubation, Y = Young in colony.

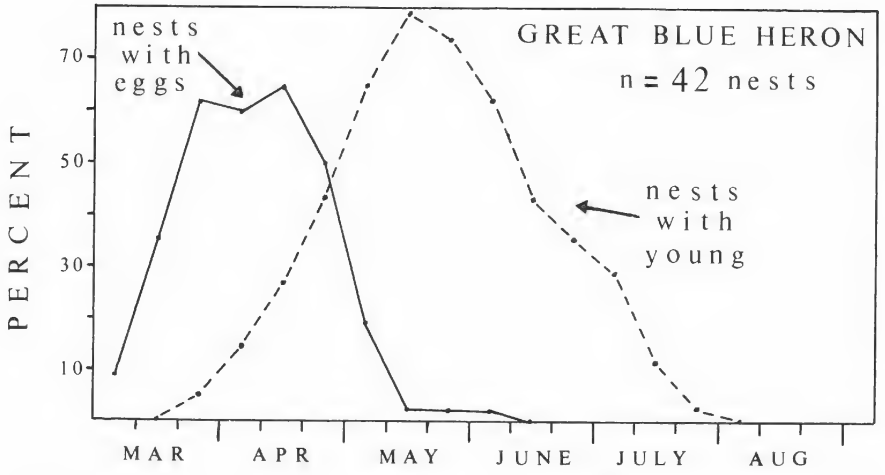


Figure 3. Chronological variation in percentage of 42 Great Blue Heron nests containing eggs or young, Columbia River colonies—1978.

TABLE 2. Chronological changes in nest contents of Caspian Tern and California and Ring-billed Gull nests during April-June 1978.

| Species | Date | No. nests examined | Nest Contents (%) | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Eggs | | | | | |
| | | | 0 | 1 | 2 | 3 | 4 | Chicks |
| Gullsa | 24 Apr | 182 | 69.6 | 20.3 | 7.1 | 3.3 | | |
| | 28 Apr | 415 | 27.7 | 22.2 | 25.5 | 24.6 | | |
| | 18 May | 1407 b | | 6.9 | 36.7 | 51.8 | 1.2 | 3.4 |
| | 31 May | 156 b | | 7.1 | 20.5 | 19.9 | | 52.6 |
| Caspian | 17 May | 190 | | 8.4 | 41.6 | 43.7 | 6.3 | 0 |
| Tern | 2 June | 210 | | 11.9 | 30.5 | 10.0 | 3.4 | 44.3 |

aSample counts from colonies in The Dalles and John Day reservoirs.

bSome recently initiated nests not yet containing eggs probably were present during these counts but activity of adults and chicks prevented certain identification of such nests.

period between arrival at colonies and initiation of egg-laying was considered (Fig. 2). Some very young nestlings were in nests until about 30 June, but young produced by the main breeding contingent of both species were out of nests by mid-June.

The two species of terns contrasted sharply in their breeding sequences. Caspian Terns occupied their colony for the briefest period of all species, initiating nests soon after arrival in mid-April and fledging young by late July (Fig. 2). The entire breeding effort was concentrated into an approximate 95-day period; 44 percent of the nests had hatched by 2 June (Table 2), and no young remained in nests beyond 20 June. A few Caspian Terns may have nested somewhat later, as indicated by a single nest with two eggs found on 14 July; however, this nest was exceptional and was not entered in the chronology record. Forster's Terns arrived latest and were asynchronous within the colony, exhibiting extended phases relative to the small number of nests (Fig. 2). The possibility of an early and late breeding complement was suspected but not as-

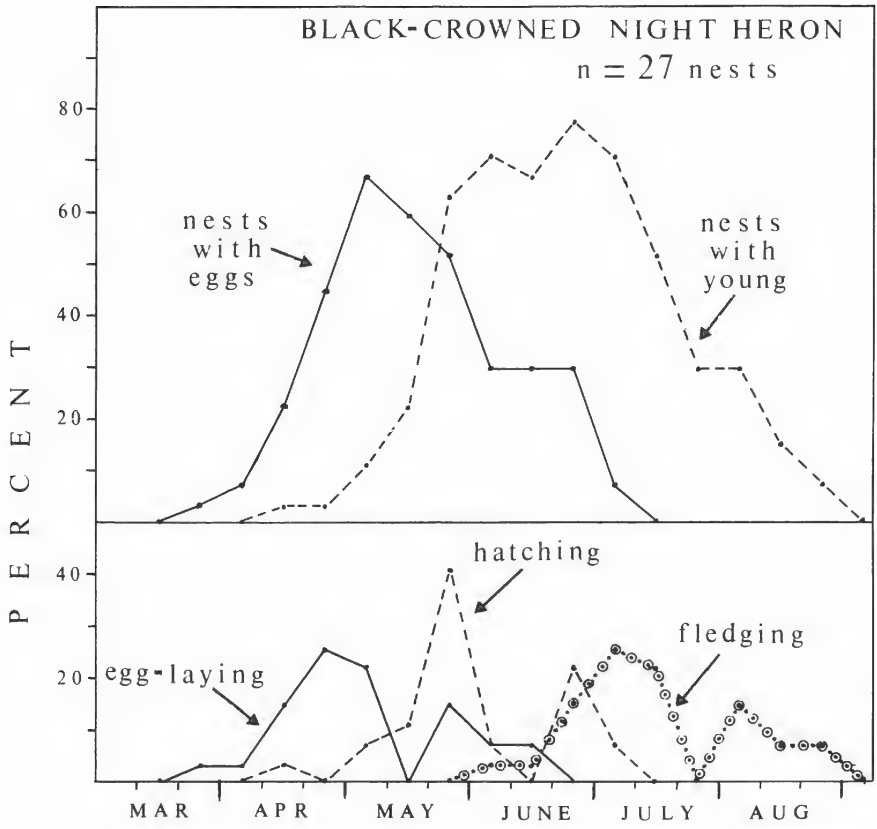


Figure 4. Timing of three reproductive phases and changes in nest contents for 27 Black-crowned Night Heron nests in the Threemile Canyon Island colony, Columbia River—1978.

certained. Young Forster's Terns left the nests when a few days old and possibly left the colony site prior to attaining flight (dashed line in Fig. 2).

Great Blue Herons were asynchronous both within and among colonies; thus, egg-laying through fledging spanned nearly 6 months from late February to mid-August (Fig. 3). Despite asynchrony within colonies, most reproductive efforts were concentrated in the early half of each phase, and peaks were observed in the percentages of nests that contained eggs or young during successive 10-day intervals (Fig. 3). However, asynchrony between colonies prevented the expression of a single 10-day peak period for each phase. Limited observations at colonies 1, 2, and 3 indicated that the chronology computed for Great Blue Herons was applicable at least as far west as Portland.

Black-crowned Night Herons were asynchronous within colonies, thus prolonging egg-laying through hatching from late March to mid-July (Fig. 2). This asynchrony was exemplified by the variable timing in the progression of reproductive phases and by the extended period during which nests contained eggs or young (Fig. 4). However, night herons were highly synchronous among colonies, exhibiting essentially the

same chronological periods for colonies 9 and 13 that were about 80 km (straight line) apart. The slight bimodality present in the estimated chronological timing (Fig. 4) may have represented an early and late breeding contingent as no major renesting effort was detected.

#### Discussion

The number of nests counted during this study represents the most substantial census coverage to date for this area. These counts indicated that numbers of all species were stable to increasing during the study and relative to previous surveys (Tabor, 1976). However, substantial shifts in locations of gull colonies had occurred since earlier studies (Broadbooks, 1961; Hanson, 1963) as discussed by Conover *et al.* (1979). Great Blue Herons were at least as numerous near colonies discussed by Nehls (1972) and Henny and Kurtz (1978), although colony populations had shifted slightly. Colony sites 10 and 12 were the same as the dead cottonwoods and small, rocky island discussed by Henny and Kurtz. We did not examine single heron nests in navigation markers during this study. Black-crowned Night Heron, Caspian Tern, and Forster's Tern colonies generally were stable in size and location. Additional small colonies of Forster's Terns and Black-crowned Night Herons may have existed in the study area but were not found.

Reproductive phases observed during this study generally agreed with limits previously reported for herons (Palmer, 1962; Pratt, 1970), gulls (Johnston and Foster, 1954; Broadbooks, 1961; Vermeer, 1970), and terns (Bent, 1921; DeGroot, 1931; Sibley, 1953). However, our data for Great Blue Herons revealed less synchrony among colonies than that observed by Werschkul *et al.* (1977). This contrast may have resulted in part from our greater reliance on estimates from backdating and their observation of variable time periods from peak hatch to peak fledging. Minor contrasts existed for gulls (Johnston, 1956; Vermeer, 1970) and Caspian Terns (DeGroot, 1931), but these variations easily could have represented seasonal and latitudinal variation.

Breeding by Great Blue Herons and Black-crowned Night Herons extended from February through August, but susceptibility to water fluctuations during this period was negated because most nest sites (trees and sagebrush) were above projected water levels. Indirect impacts could occur if altered water levels changed food availability during the 5-month period from initial hatching to final fledging for these two species. The effects of food availability remain to be studied because data regarding feeding routines of herons along the Columbia River are not presently available.

Gulls, terns, and about 10 pairs of night herons nested on or near ground at elevations subject to inundation at predicted future water levels. Observations at colony 9 in 1977 revealed that inundation of some active gull nests occurred under existing operating regimes in June. The impact of future water fluctuations would depend on water levels reached, time period, and species of concern. The proportion of gull nests affected would be minor because of the large breeding population, but the proportional effects on tern and night heron nests could be more substantial because of their limited occurrence. Ring-billed Gulls and Forster's Terns would be affected most easily because they tend to nest closest to water level (Hanson, 1963; Wash. Dept. of Game, unpubl.

data). Time of vulnerability could begin as early as late March if inundation interrupted courtship and site selection.

Other implications of these data concern the timing of breeding surveys designed to enumerate colonial nesters in the Pacific Northwest. The lengthy reproductive phases necessitate the appropriate timing of surveys to maximize counts relative to actual numbers of breeding pairs, to maintain comparability among years, and to reduce census confusion introduced by juvenile birds in colonies. The most appropriate time for on-site counts would be when the main breeding contingent is well into incubation or hatching is just beginning, so that nest initiation is near maximum and chances of desertion are minimized. Counts could be conducted slightly later if banding operations also were planned.

Analyses of chronologies revealed that appropriate survey times do not coincide for all species considered. Reproductive phases overlapped sufficiently for gulls and Caspian Terns to warrant a common census period (20-25 May in 1978). The extended phases and possible early and late breeding contingents exhibited by Forster's Terns, however, suggest the need for two counts, one about 25 to 30 May and one 25 to 30 June. A single count between 5 and 15 June would likely produce sufficient accuracy for most purposes if survey time were limited. The asynchrony and extended length of phases exhibited by both species of herons negates a single count, and two counts are recommended for accuracy. For Great Blue Herons, 25 March to 5 April and 1 to 10 June appeared to be most appropriate. For Black-crowned Night Herons, 15 to 25 April and 10 to 20 June appeared most appropriate for censusing. To simplify field work, common survey times (5 to 15 April and 5 to 15 June) could be used for the herons with some reduction in accuracy. The dates used above reflect the 1978 breeding regime and would be subject to change with annual variations in breeding sequences. Brief preliminary examinations of representative colonies by field personnel could establish necessary corrections each year based on initiation of egg-laying.

Much work remains to be accomplished concerning colony dynamics and reproduction of colonial nesting birds in the Pacific Northwest. Timing of trend counts especially should be based on critical consideration of nesting chronologies. The data presented herein should permit more timely examination of colonies by researchers and managers working with these species on and near the Columbia River.

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# Relative Capacities of Filamentous and Non-filamentous Bacteria from Two Forest Soils To Inhibit Phellinus weirii in Culture

**Abstract**

Alder and conifer soil were examined for *Streptomyces* spp. and non-filamentous bacteria antagonistic to *Phellinus weirii*. Conifer soil supported higher populations *Streptomyces* spp. and higher percentage of *Streptomyces* species antagonistic to *P. weirii* than did alder soil. The populations of non-filamentous bacteria were low in both soils. Alder soil, however, had a higher percentage of non-filamentous bacteria antagonistic to *P. weirii* than did conifer soil. Identified *Streptomyces* show that different species are present in each soil type.

## Introduction

*Phellinus weirii* (Murrill) Gilbertson [= *Poria weirii* (Murrill) Murrill] causes serious root rot of many species of native conifers in western North America. The fungus can survive for many years in stumps and roots of dead and living trees, and it may infect roots of adjacent host trees when ectotrophic mycelia pass from one to another at points of root contact.

Some evidence suggests that damage to susceptible conifers is suppressed by the presence of red alder, *Alnus rubra* Bong. (Trappe, 1972; Nelson *et al.* 1978). Alder soils contain phenolic compounds shown to inhibit growth of *P. weirii* in vitro (Li *et al.*, 1972) and high levels of nitrogen including $NO_3$ (Franklin *et al.*, 1968), a form of N not utilized by *P. weirii* (Li *et al.*, 1967). Researchers have also shown significant differences in microbial populations between alder and conifer soil (Lu *et al.*, 1968; Wicklow *et al.*, 1974). The relative numbers or percentage of microbes antagonistic to *P. weirii*, however, have not been reported. Soil microbes, in addition to nitrogen and phenolic compounds, might influence disease development. In this study, we examine differences in populations of *Streptomyces* and non-filamentous bacteria antagonistic to *P. weirii* in adjacent stands of red alder and of mixed conifers, primarily Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco].

This study was conducted at Cascade Head Experimental Forest of coastal Oregon, an area chosen for its history of intensive research and available scientific information.

## Methods and Materials

Three soil samples were collected from one alder stand and from one conifer stand at two-month intervals for one year. Each sample consisted of three sub-samples taken approximately 60 cm from the base of a tree to a depth of 64 cm after the first 5 cm of top litter had been removed. The soil was immediately taken to the laboratory and screened through a 6-mm sieve.

Soil dilution plates (1:50,000 dil.) were made in triplicate from 20 gm each of the soil samples using sodium albuminate agar (pH 6.8) as the selective medium for *Streptomyces* and non-filamentous bacteria. The plates were incubated at 28° C for eight days and colonies counted. A double-layer plate technique (Li *et al.*, 1969) was used to test antagonism towards *P. weirii*. The fungus was first grown in malt broth, then the mycelium was washed in sterile, distilled water, and homogenized. One ml of the homogenate was pipetted into each petri plate and 10 ml of 1 percent water-agar was poured on top and allowed to solidify. Ten ml of malt yeast peptone (MYP) agar medium was layered over the water-agar and the surface inoculated with bacterial colonies, randomly selected from the dilution plates. Double-layer plates were incubated at 26° C for two weeks, and antagonism was recorded if a zone of inhibition was produced around a bacterial colony (Fig. 1).

Totals of 2144 *Streptomyces* colonies from conifer soil and 1571 colonies from alder soil were tested for their antagonism to *P. weirii*. Of the non-filamentous bacteria,

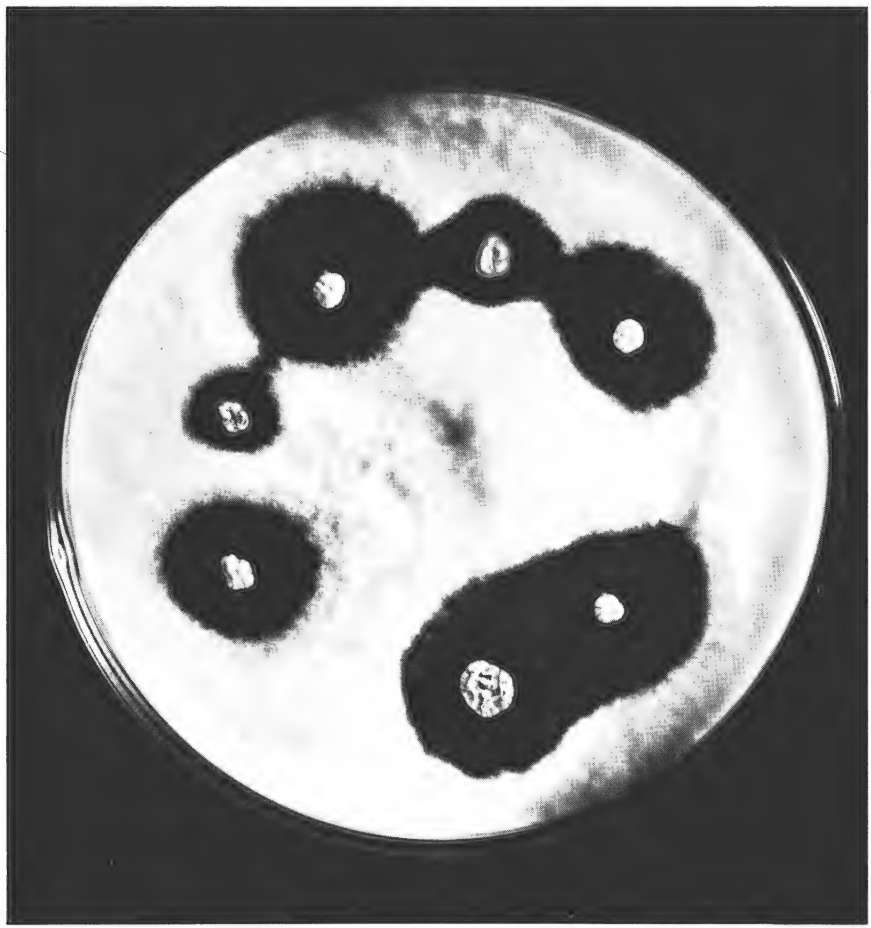

Figure 1. Inhibition of *P. weirii* by *Streptomyces* isolated from conifer soil.

462 from conifer soil and 797 from alder soil were tested for their antagonism to *P. weirii.*

Differences in the percentages of antagonistic *Streptomyces* and non-filamentous bacteria between the two soil-types were tested for significance by two factor analysis of variance, "ANOVA" (Neter and Wasserman, 1974).

Twenty colonies of *Streptomyces* antagonistic to *P. weirii* were randomly selected from cultures grown from the October samples taken from each of the two stands. These organisms were identified by methods, and on media, described by Shirling and Gottlieb (1966, 1968 a, 1968 b, and 1969) as modified by Kuster (1972). Color of aerial mycelium and reverse side of mycelium, color of soluble pigment, melanin reaction, and morphology of sporophores and spores noted. Carbohydrate utilization and growth rates were determined with sucrose, D-mannitol, L-arabinose, D-cylose, D-fructose, rhamnose, I-inositol, and raffinose. Glucose agar was used as a positive control and media without carbohydrate as a negative control. Electron micrographs were used to determine sporophore and spore morphology.

#### Results

The percentage of *Streptomyces* isolates antagonistic to *P. weirii* was significantly higher ($p \leq .05$) in those isolated from conifer soil than from alder soil at all sampling times (Fig. 2). Twenty-seven percent of the *Streptomyces* from conifer soil and 14 percent of the *Streptomyces* from alder soil were antagonistic to *P. weirii.* The proportion of antagonists differed among the months of isolation ($p \leq .05$), but the greatest mean responses for both conifer (48 percent) and alder (28 percent) sites occurred in October.

Conifer soil, in addition to having the higher percentage of antagonistic *Streptomyces*, had a higher total number of *Streptomyces* isolates for the two sampling times when counts per gram of soil were calculated: $2.0 \times 10^5$/g in January and $1.8 \times 10^6$/g in April. The population in alder soil was $8.0 \times 10^4$/g in January and $1.5 \times 10^6$/g in April.

None of the 40 antagonistic *Streptomyces* isolates identified from October samples were common to both soils. Of the 20 conifer soil isolates, 15 were identified as *S. parvulus* Waksman and Gregory; 4 as *S. aureomonopodiales* Krasilnikov and Yuan; and 1 as *S. hawaiiensis* Cron, Whitehead, Hooper, Heinemann and Lein. From the 20 alder isolates, 11 were identified as *S. plicatus* (anon.); 4 as *S. gelaticus* Waksman and Henrici; 4 as *S. atroolivaceus* Preobrazhenskaya, Blinov and Ryabova; and 1 as *S. rochei* Berger, Jampolsky and Goldberg.

In contrast to *Streptomyces* results, a significantly greater proportion ($p = .05$) of non-filamentous bacteria from alder soil were antagonistic to *P. weirii* (21 percent) than from conifer soil (4 percent) for six sampling times combined (Fig. 2). However, non-filamentous bacteria were far less numerous (organisms/g soil) than *Streptomyces* in either soil. The population of non-filamentous bacteria in alder soil was $5.6 \times 10^4$/g in January and $2.3 \times 10^5$/g in April. In conifer soil it was $3.1 \times 10^4$/g in January and $1.3 \times 10^5$/g in April.

#### Discussion

We did not substantiate that the alder soil we sampled had antagonistic populations sufficient to inhibit *P. weirii.* On the contrary, our tests showed that the conifer soil supported higher populations of *Streptomyces* with a higher percentage of *Streptomyces*

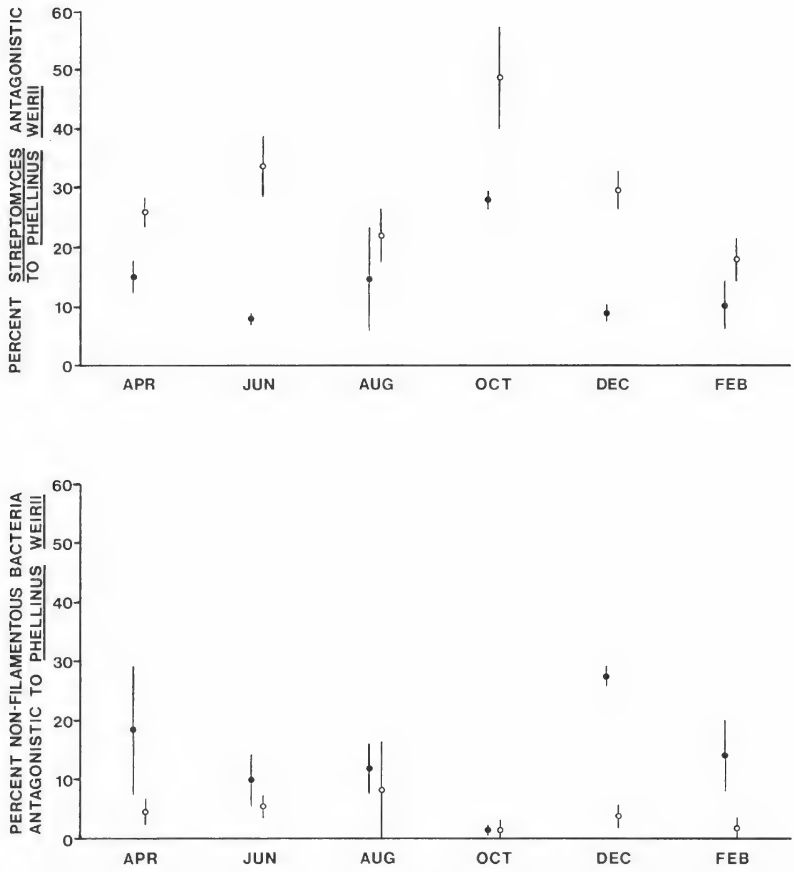


Figure 2. Comparison of the percentage of *Streptomyces* and non-filamentous bacteria antagonistic to *P. weirii* in conifer and alder soil. Open dot represents the mean value in conifer soil. Closed dot represents the mean value in alder soil. The bar lines denote standard error.

isolates antagonistic to *P. weirii* than did the alder soil. The difference in populations might be attributed to the soil pH (5.3 in conifer vs. 4.6 in alder). Normally, in agricultural soils, it is considered that a soil pH of 5.0 or less will limit the growth of most strains of actinomycetes (Alexander, 1961), and many forest soils of pH 4.6 or less have only small numbers of actinomycetes (Jensen, 1930). Alder soil, however, did have a greater proportion of non-filamentous bacteria antagonistic to *P. weirii*; but owing to the relatively small populations, it appears these bacteria had little influence on the total antagonistic microbial population.

Christensen *et al.* (1962), Christensen and Whittingham (1965), and Wicklow *et al.* (1974) have shown that fungal populations of the soil reflect the species composition of higher vegetation. Wicklow *et al.* (1974) also found relatively few dominant species of fungi in alder and conifer stands. Our results parallel these findings in that we found both a distinctly different antagonistic *Streptomyces* population in conifer vs. alder soil and an apparent dominance by relatively few species, none of which were

common to both soils. These results suggest a very specific and definable microbial community may exist in forest soils related to the dominant vegetative communities growing there.

The alder soil studied here was low in populations of what Baker and Cook (1974) called "resident antagonists," (bacteria and actinomycetes). Therefore, the opportunities for biological control based on fungistasis and antagonism found in this soil are probably reduced as compared to the conifer soil. Since sample sites were limited to a single area, conclusions cannot be broadly extrapolated. More intensive work needs to be done in soils under different tree species to determine whether the differences in microbial populations are consistent and can be related to the behavior of *P. weirii.*

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# Grazing, Crested Wheatgrass, and Bird Populations in Southeastern Idaho

**Abstract**

Populations of nesting and non-nesting birds were examined and compared in grazed and ungrazed habitats dominated by sagebrush and crested wheatgrass. Sheep grazing in a sagebrush community did not alter the density or the diversity of nesting bird populations. Planting a former sagebrush range with crested wheatgrass, with or without grazing pressures, reduced the diversity and abundance of nesting species. More species and individuals of migrant and non-nesting birds used the sagebrush habitats than the crested wheatgrass plantings. Habitat selection by birds appeared to be related to the vegetational physiognomy rather than the floral composition of the habitat.

## Introduction

Sagebrush (*Artemisia* spp.) was once the dominant vegetation over 60-100 million ha of the western rangelands in the United States (Beetle, 1960; Sturges, 1973). In historic times, the primary use of sagebrush range has been for livestock grazing. Efforts to improve the quality of rangelands for livestock traditionally involved the chemical or mechanical control of sagebrush followed by planting grass species such as crested wheatgrass (*Agropyron cristatum* and *A. desertorum*). In this century, 10-12 percent of the sagebrush-dominated rangelands were thusly altered (Vale, 1974). Research evaluating management practices on historic sagebrush range has focused mainly on the nutritive value and carrying capacity for livestock (Cook and Harris, 1952; Cook and Stoddart, 1953; Frischknecht *et al.*, 1953; Noll, 1955; McWilliams and Van Cleave, 1960; Pearson, 1965; Laycock, 1967; Frischknecht and Harris, 1968; McKendrick and Sharp, 1971), or on the effects of livestock grazing and sagebrush control on big game species (Anderson, 1969; Mackie, 1970; Peterson, 1971) and Sage Grouse (*Centrocercus urophasianus*) (Patterson, 1952; Klebenow, 1970; Martin, 1970). These studies indicate that while sagebrush conversion projects generally improve the native habitat for livestock use, large scale sagebrush control projects and/or competition with livestock adversely affect populations of deer (*Odocoileus hemionus*), wapiti (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and Sage Grouse during some seasons.

With the exception of Sage Grouse, few studies have been published on the response of avifauna to sagebrush management and/or grazing pressures (Feist, 1968; Walcheck, 1970; Best, 1972; Schroeder and Sturges, 1975). This study compared the species diversity and relative density of nesting and non-nesting birds in four

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areas of different land management on the Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho.

#### Study Areas

The INEL Site occupies 2315 km$^2$ of the upper Snake River Plain approximately 48 km west of Idaho Falls, Idaho. The Site is a National Environmental Research Park dominated by big sagebrush (*A. tridentata*) (Harniss and West, 1973). Parts of the park have been planted with crested wheatgrass, and livestock grazing is permitted on about 60 percent of the area (Fig. 1). Two of the four study areas were dominated by sagebrush, and two were former sagebrush range reseeded with crested wheatgrass. One sagebrush and one crested wheatgrass area were located just within the southern boundary of the INEL Site (Fig. 1). Crested wheatgrass was planted here in 1958 or 1959 (INEL Site records vary) after the native vegetation was removed by discing. These two areas were contiguous and were grazed by 1000-1200 domestic sheep each spring since 1960. These areas are referred to as GRAZED SAGE and GRAZED CWG.

The other study areas were approximately 12 km northwest of the GRAZED sites (Fig. 1). The sagebrush here (UNGRAZED SAGE) was grazed periodically prior to 1950. This area, with 25 years to recover from any grazing impacts, served as the control plot for the study. The adjacent crested wheatgrass planting (UNGRAZED CWG) was seeded in 1960 after winter flooding inundated and killed the native vegetation (A. Olson, pers. comm.). Domestic livestock were never pastured in this planting.

Both SAGE study areas and the GRAZED CWG occupied over 100 km$^2$. The UNGRAZED CWG was the largest tract of its kind we found on the INEL Site, but was less than 1 km$^2$.

#### Methods and Materials

The plant species composition and canopy coverage were estimated in each area along 4-100 m transect lines. Sampling frames, 20 x 50 cm (Daubenmire, 1959), were placed at 2.5 m intervals along each transect. Six cover classes (0-5 percent, 6-25 percent, 26-50 percent, 51-75 percent, 76-95 percent, 96-100 percent) were used to estimate the percent canopy coverage for each species. The average canopy coverage for each species was used to calculate the percent similarity (PS) (Orloci, 1967) among the study areas with the formula:

$$PS = 100 \left\{ 1 - \left[ \sum_{i=1}^{s} \left( \frac{X_{s,B}}{\left( \sum_{i=1}^{s} X_{s,B}^2 \right)^{1/2}} - \frac{X_{s,A}}{\left( \sum_{i=1}^{s} X_{s,A}^2 \right)^{1/2}} \right)^2 \right]^{1/2} \right\}$$

where X was the average coverage value for each individual species(s) from the areas being compared (A and B).

Nesting bird species were examined using the singing male technique (Williamson, 1964) and the flushed male mapping procedure (Wiens, 1973). A 4-ha grid

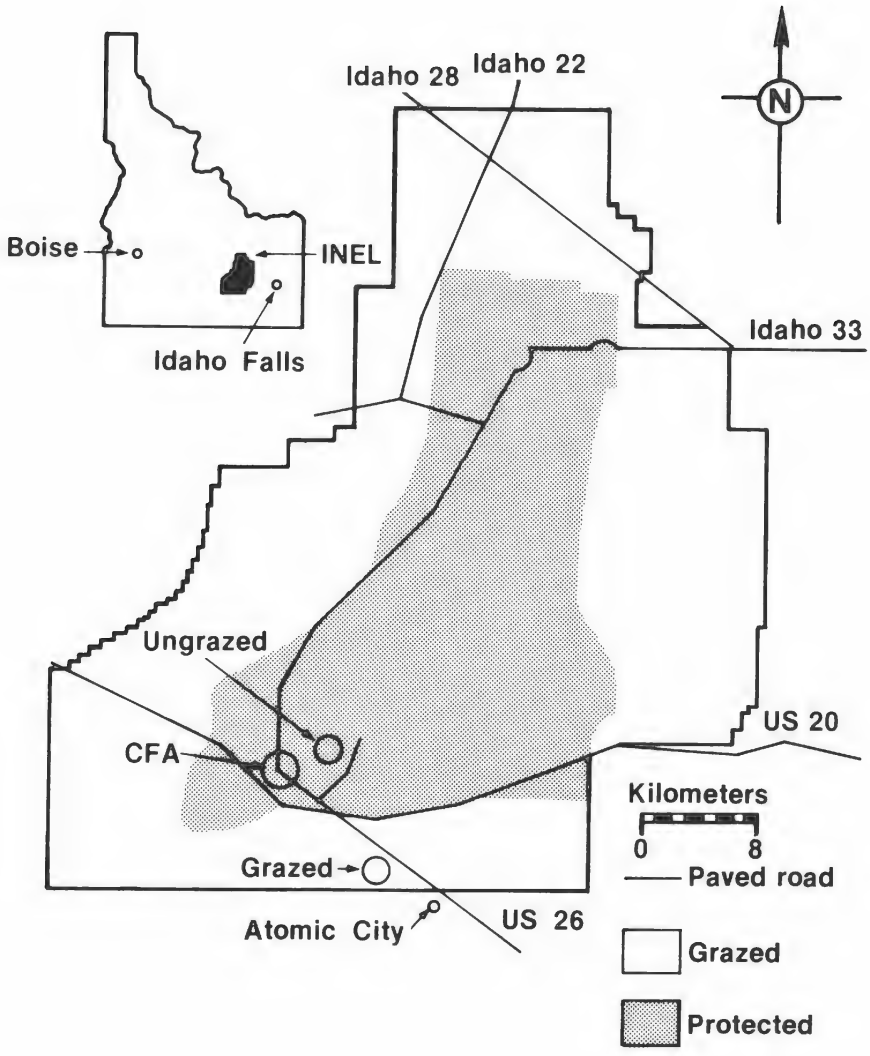


Figure 1. Grazed and ungrazed study areas on the INEL Site. Each area included a habitat dominated by big sagebrush and one dominated by crested wheatgrass. The portions of the INEL Site protected from livestock use are shown.

was established in each study area with 1.8-m tall wood stakes placed at 50-m intervals. The grid pattern in the two GRAZED study areas was a square 200 m on a side. The limited amount of area in the UNGRAZED CWG, and the unusual configuration of the adjacent UNGRAZED SAGE, prohibited establishing square grids in these areas (Fig. 2). All grid stakes were color-coded with plastic flagging to enhance accurate mapping of territories and location of nests.

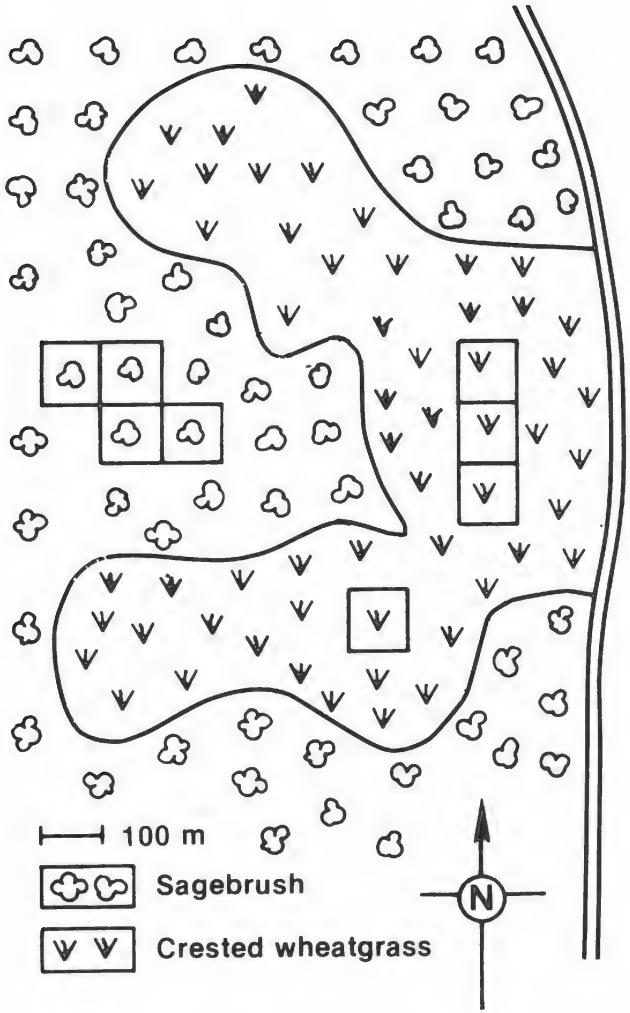


Figure 2. The configuration of the 4-ha UNGRAZED SAGE and UNGRAZED CWG. A paved road is at the extreme right.

Two researchers visited the study plots every other day during the 1976 and 1977 nesting seasons (mid-March through mid-July). One would examine both GRAZED areas while the other spent equal time in the UNGRAZED plots, alternating sites each visit. Investigation usually began 0.5 hr before sunrise and continued until the birds ceased singing, which was generally 4-6 hrs after sunrise. Additionally, evening visits were made on an irregular basis during the breeding season, and fortnightly examinations were conducted at various times of the day during the non-nesting season. Territory maps were made for each territorial bird (Reynolds and Rich, 1978), and

all nests were located by flushing a bird from its nest or by observing nest building, courtship, or food carrying behavior and then rigorously searching the area for the nest. The number and species of non-nesting birds (migrants and those nesting elsewhere on the Snake River Plain) encountered in each habitat were recorded as the relative density of these species in each study area. Differences in relative density were compared using the chi square statistic (Snedecor and Cochran, 1967).

A species diversity index (H) was calculated for nesting and non-nesting birds and for vegetation using a transformation of the Shannon equation (Zar, 1974):

$$H = (N \ln N - \Sigma f_i \ln f_i)/N$$

where f was the number (frequency) of each species i and N was the total frequency of all species. Differences in species diversity were tested with the t-test (Hutcheson, 1970). For all statistical tests, the level of significance was $P < 0.05$.

## Results

### Vegetation

Big sagebrush was the dominant vegetation in both SAGE study areas, providing 65 percent of the total canopy coverage in the GRAZED SAGE and 41 percent in the UNGRAZED SAGE. The control area contained the greatest number of plant species (31) (Table 1) and had a species diversity index of 2.85: significantly greater than all other areas. The percent similarity (PS) of the floristic composition of the two SAGE areas was 38 percent.

Crested wheatgrass was the primary component of the GRAZED and UNGRAZED CWG habitats, providing 89 and 98 percent of the total cover respectively. The PS value for the two CWG areas was 90 percent.

### Nesting Birds

Seventy-one nests, representing 10 species, were located and monitored during the study (Table 2). There were no significant intra-area differences in the diversity or density of nesting birds between 1976 and 1977, which allowed us to pool the data over the 2-year period. The control area contained 27 nests representing 7 species, and had a species diversity index (H) of 1.67. Seven species accounted for 30 nests ($H = 1.40$) in the GRAZED SAGE. The density and species diversity of nesting birds in the two SAGE areas were not statistically different (Table 2).

Ten nests representing four species were located in the UNGRAZED CWG, but only four nests of one species (Horned Lark, *Eremophila alpestris*) were found in the GRAZED CWG. The species diversity indices were 1.19 and 0.00 respectively. Nesting density and species diversity differed significantly between the two CWG areas. Additionally, both CWG areas had a nesting density and species diversity significantly below the control (Table 2).

During the period when Horned Larks nests were found in the UNGRAZED CWG in 1976 (8-14 May), sheep were pastured in the grazed study areas. We found no evidence of Horned Larks nesting activities in the GRAZED areas until 28 May, nearly two weeks after the sheep had been moved to a different range. In 1977, the sheep were moved two weeks earlier (1 May) as a result of deteriorating range conditions resulting from regional drought. The first Horned Lark nest found in the

TABLE 1. Frequency (f), canopy coverage (%), and species diversity of vegetation in grazed and ungrazed habitats dominated by sagebrush or by crested wheatgrass on the INEL Site.[a]

| | UNGRAZED | | | | GRAZED | | | |
|---|---|---|---|---|---|---|---|---|
| | SAGEBRUSH | | CRESTED WHEATGRASS | | SAGEBRUSH | | CRESTED WHEATGRASS | |
| | % | f | % | f | % | f | % | f |
| **Crypantha watsoni** | 0.2 | 5 | | | | | | |
| **Lappula redowskii** | 0.1 | 5 | | | | | | |
| **Opuntia polyacantha** | 1.3 | 13 | | | | | | |
| **Chenopodium leptophyllum** | 0.6 | 17 | | | | | | |
| **Halogeton glomeratus** | | | | | 1.4 | 43 | 3.9 | 13 |
| **Artemisia tridentata** | 17.00 | 105 | | | 25.0 | 113 | 0.5 | 5 |
| **Aster** sp. #1 | +[b] | 1 | | | | | | |
| **Aster** sp. #2 | + | 1 | | | | | + | 1 |
| **Aster scopulorum** | 0.7 | 23 | | | | | | |
| **Chaenactis douglasii** | 0.3 | 4 | | | | | | |
| **Chrysothamnus nauseosus** | 0.2 | 3 | | | 1.6 | 15 | 0.4 | 5 |
| **Erigeron pumilus** | 0.3 | 11 | | | | | | |
| **Lygodesmia grandiflora** | + | 1 | | | | | | |
| **Arabis sparsiflora** | 0.3 | 11 | 1.0 | 15 | | | | |
| **Descurainia sophiam** | + | 1 | | | | | | |
| **Lepidium perfoliatum** | | | | | 0.2 | 2 | | |
| **Schoenocrambe linifolia** | 0.1 | 7 | | | | | | |
| **Sisynbrium altissimum** | + | 1 | | | | | | |
| **Stanleya viridiflora** | + | 1 | | | | | | |
| **Menziesia glabella** | + | 1 | | | | | | |
| **Agropyron cristatum** | 1.9 | 15 | 52.0 | 160 | | | 39.4 | 154 |
| **Agropyron spicatum** | 6.0 | 35 | | | | | | |
| **Bromus tectorum** | 0.7 | 8 | | | | | | |
| **Oryzopsis hymenoides** | 5.2 | 34 | 0.2 | 3 | | | | |
| **Poa sandbergii** | 1.8 | 16 | | | 9.2 | 93 | | |
| **Sitanion hystrix** | 3.0 | 35 | | | | | | |
| **Astragalus purshii** | 1.9 | 16 | | | | | | |
| **Allium geyeri** | + | 1 | | | | | | |
| **Sphaeralcea munroana** | + | 1 | | | | | | |
| **Eriastrum sparsiflorum** | + | 3 | | | | | | |
| **Gilia leptomeria** | + | 3 | | | | | | |
| **Phlox hoodii** | | | | | 1.4 | 14 | | |
| **Eriogonum cernum** | + | 1 | | | | | | |
| **Cordylanthus ramosus** | + | 1 | | | | | | |
| Total number of species | 31 | | 3 | | 9 | | 5 | |
| Total percent of coverage | 41.6 | | 53.2 | | 38.7 | | 44.1 | |
| Species diversity (H) | 2.85a | | 0.37b | | 1.17c | | 0.54d | |

[a]Species diversities followed by a different letter are different ($P < 0.05$).

[b]Percent coverage less than 0.1%.

GRAZED CWG that year was on 12 May, again almost two weeks after the sheep had been moved.

### Non-nesting Birds

Thirty-six species of non-nesting birds were recorded in one or more of the study areas (Table 3). The species diversity indices followed the same pattern determined for nesting birds with *UNGRAZED SAGE = GRAZED SAGE > UNGRAZED CWG > GRAZED CWG* (Table 3). Significantly fewer non-nesting birds were recorded in the two CWG areas than in the control area, but significantly more were found in the GRAZED SAGE than in any other area.

TABLE 2. Number of nests (relative density) and species diversity of nesting birds in grazed and ungrazed habitats dominated by sagebrush (**Artemisia tridentata**) or by crested wheatgrass (**Agropyron cristatum**) on the INEL site, 1976 and 1977.[a]

| | UNGRAZED | | GRAZED | |
|---|---|---|---|---|
| SPECIES | SAGEBRUSH | CRESTED WHEAT-GRASS | SAGEBRUSH | CRESTED WHEAT-GRASS |
| Sage Grouse[b] **Centrocercus urophasianus** | 0 | 0 | 1 | 0 |
| Mourning Dove **Zenaida macroura** | 5 | 0 | 1 | 0 |
| Short-eared Owl **Asio flammeus** | 1 | 1 | 0 | 0 |
| Loggerhead Shrike **Lanius ludovicianus** | 1 | 0 | 1 | 0 |
| Horned Lark **Eremophila alpestris** | 0 | 4 | 1 | 4 |
| Western Meadowlark **Sturnella neglecta** | 1 | 4 | 0 | 0 |
| Sage Thrasher[b] **Oreoscoptes montanus** | 8 | 0 | 14 | 0 |
| Vesper Sparrow **Pooecetes gramineus** | 0 | 1 | 0 | 0 |
| Sage Sparrow[b] **Amphispiza belli** | 7 | 0 | 9 | 0 |
| Brewer's Sparrow[b] **Spizella breweri** | 4 | 0 | 3 | 0 |
| RELATIVE DENSITY | 27a | 10b | 30a | 4b |
| SPECIES DIVERSITY | 1.67a | 1.19b | 1.40a | 0.00c |

[a]Relative densities and species diversity indices not followed by the same letter are different ($P < 0.05$).

[b]Sagebrush obligate (Braun **et al.** 1976).

TABLE 3. Number of observations (relative density) and species diversity of non-nesting birds in grazed and ungrazed habitants dominated by sagebrush or by crested wheatgrass on the INEL Site. March, 1976-August, 1977.[a]

| | UNGRAZED | | GRAZED | |
|---|---|---|---|---|
| SPECIES | SAGEBRUSH | CRESTED WHEATGRASS | SAGEBRUSH | CRESTED WHEATGRASS |
| Red-tailed Hawk **Buteo jamaicensis** | 2 | 2 | 1 | 1 |
| Swainson's Hawk **Buteo swainsoni** | 1 | 1 | 5 | 1 |
| Rough-legged Hawk **Buteo lagopus** | 2 | 1 | 1 | 0 |
| Ferruginous Hawk **Buteo regalis** | 2 | 1 | 1 | 0 |
| Northern Harrier **Circus cyaneus** | 12 | 10 | 18 | 10 |
| Prairie Falcon **Falco mexicanus** | 2 | 0 | 0 | 0 |
| Kestrel **Falco sparverius** | 1 | 1 | 4 | 2 |
| Ring-necked Pheasant **Phasianus colchicus** | 0 | 0 | 3 | 1 |
| American Coot **Fulica americana** | 1 | 0 | 0 | 0 |
| Killdeer **Charadrius vociferus** | 0 | 0 | 3 | 2 |
| Long-billed Curlew **Numenius americanus** | 1 | 1 | 0 | 1 |
| Poorwill **Phalaenoptilus nuttallii** | 0 | 0 | 1 | 0 |
| Common Nighthawk **Chordeiles minor** | 2 | 2 | 1 | 0 |
| Common Flicker **Colaptes auratus** | 1 | 1 | 2 | 0 |
| Western Kingbird **Tyrannus verticalis** | 0 | 1 | 2 | 0 |
| Say's Phoebe **Sayornis saya** | 0 | 0 | 1 | 0 |
| Gray Flycatcher **Empidonax wrightii** | 1 | 0 | 0 | 0 |
| Violet-green Swallow **Tachycineta thalassina** | 0 | 0 | 1 | 0 |
| Rough-winged Swallow **Stelgidopteryx ruficollis** | 4 | 0 | 2 | 2 |
| Barn Swallow **Hirundo rustica** | 22 | 4 | 16 | 4 |
| Cliff Swallow **Petrochelidon pyrrhonota** | 0 | 1 | 4 | 2 |
| Common Raven **Corvus corax** | 1 | 1 | 17 | 5 |
| Common Crow **Corvus brachyrhynchos** | 1 | 0 | 0 | 0 |
| Rock Wren **Salpinctes obsoletus** | 0 | 0 | 1 | 0 |
| American Robin **Turdus migratorius** | 2 | 0 | 0 | 0 |
| Yellow Warbler **Dendroica petechia** | 0 | 0 | 1 | 0 |
| Red-winged Blackbird **Agelaius phoeniceus** | 0 | 2 | 0 | 0 |
| Brewer's Blackbird **Euphagus cyanocephalus** | 22 | 12 | 22 | 5 |

TABLE 3. (Continued)

| | | | | |
|---|---|---|---|---|
| Brown-headed Cowbird **Molothrus ater** | 4 | 1 | 32 | 1 |
| Pine Siskin **Spinus pinus** | 0 | 0 | 2 | 0 |
| American Goldfinch **Spinus tristis** | 4 | 0 | 0 | 0 |
| Lark Bunting **Calamosphiza melanocorys** | 1 | 0 | 0 | 0 |
| Savannah Sparrow **Passerculus sandwichensis** | 0 | 0 | 0 | 2 |
| Chipping Sparrow **Spizella passerina** | 0 | 0 | 1 | 0 |
| White-crowned Sparrow **Zonotrichia leucophrys** | 1 | 1 | 3 | 0 |
| Snow Bunting **Plectrophenax nivalis** | 6 | 18 | 16 | 24 |
| RELATIVE DENSITY | 96a | 61b | 161c | 63b |
| SPECIES DIVERSITY (H) | 2.47a | 2.33b | 2.61a | 2.11c |

[a]Relative densities and species diversity indices followed by a different letter are different ($P < 0.05$).

### Discussion and Conclusions

The response of avian populations to different land management practices in historic sagebrush rangeland has received little attention in the literature. Sage grouse, Sage Thrashers (*Oreoscoptes montanus*), Brewer's Sparrows (*Spizella breweri*), and Sage Sparrows (*Amphispiza belli*) are considered sagebrush obligates, dependent on the sagebrush environment for nesting habitat (Braun *et al.*, 1976). Our data bear out this hypotheis. No nests of these species were located outside of the habitats dominated by sagebrush. Sagebrush obligates accounted for 70 percent of the nests in the control area and 90 percent of the nests in the GRAZED SAGE. Although the data are not conclusive, apparently those species not restricted to the sagebrush habitat may be more sensitive to the effects of grazing than sagebrush obligates. Alternatively, these non-obligate species may be demonstrating their ability to utilize different habitats when under stress, an adaptative advantage not shared by sagebrush obligates.

Mourning Doves (*Zenaida macroura*) are ubiquitous game birds in Idaho, nesting in trees, bushes, and on the ground (Larrison *et al.*, 1967). In this study, all dove nests were on the ground and placed under the crown of sagebrush plants. One hundred sixty observations of doves were recorded in the sagebrush habitats and 65 in CWG habitats, indicating that doves prefer sagebrush to crested wheatgrass plantings and may require brushy habitat for nesting activities in certain areas of the west.

The plant species diversity was reduced in the habitat dominated by sagebrush and grazed by sheep. This diversity was not accompanied by a reduction in the density or the diversity of either nesting or non-nesting birds. Crested wheatgrass plantings also exhibited a significant reduction in plant species diversity concomitant with significant reductions in both the diversity and density of nesting birds. Thus, the general pattern of habitat use by nesting species appears to be related to the basic physiognomy of the vegetation, with those species nesting in sagebrush habitats rarely if ever nesting in crested wheatgrass plantings, and vice versa. This pattern also seems to be true for the number of non-nesting birds: more migrants and birds nesting off the study areas used the habitats dominated by sagebrush than used crested wheatgrass plantings.

The diversity and density of nesting birds was further reduced in the area planted with crested wheatgrass and grazed by sheep, indicating a synergistic effect. Also, grazing appeared to result in a physical disturbance delaying the onset of nesting activities by Horned Larks.

In conclusion, spring grazing by domestic sheep appears to be compatible with

nesting and non-nesting bird populations in sagebrush-dominated habitats. However, planting a former sagebrush range with crested wheatgrass dramatically alters the structure of the plant community, rendering the habitat unsuitable for a diverse and abundant avifauna.

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# Microrelief and Vegetation Development on Coal Tailings in Southeast British Columbia

**Abstract**

On a one-year-old reclaimed tailings pond disturbed by vehicles, floods, and animal activity, total vegetation cover was greatest in hollows, least on ridges and west exposures, and intermediate on north, south, and east exposures. A similar pattern, varying in degree, existed for cover of individual species. Height growth within individual species varied little between microsites. Optimum microtopographic relief appears to be 20-30 cm high with furrows 80-100 cm apart.

From an original seed mix of ten species, seven dominated including smooth brome (*Bromus inermis* Leyss.), Canada bluegrass (*Poa compressa* L.), timothy (*Phleum pratense* L.), creeping red fescue (*Festuca rubra* L.), redtop (*Agrostis alba* L.), meadow foxtail (*Alopecurus pratensis* L.), and alfalfa (*Medicago* sp.). Perennial rye (*Lolium perenne* L.) was absent. Of eight invading species all with negligible cover, four wheatgrasses (*Agropyron* spp.) grew vigorously and should be considered for subsequent seed mixes.

## Introduction

Coal tailings are the fine grained carbonaceous waste produced from the flotation separation of ground raw coal in the cleaning plant and deposited in permanent holding ponds where water dissipates, leaving large level areas of homogenous waste. Its black color and unusual water retention properties make reclamation of this waste difficult. The high heat retention by the black waste increases surface temperatures and moisture loss by evaporation. Water also infiltrates rapidly through the tailings with no replacement from the water table. Plants may therefore be damaged by insufficient moisture and high temperatures at the stem soil interface.

Through influencing relative competitive abilities of individual species, vegetation on reclaimed areas may be modified by factors such as uniformity of seed germination rates, fertilizer and mulch application, and regularity of surface condition. Although not working on mine tailings, Ayaad and Dix (1964), Money (1965), and Kershaw (1973) found that microtopographic variation affected vegetative pattern by influencing the microclimate. Microrelief allows seeds to collect in hollows and provides shade and moisture to germinating plants. Once established, these plants ameliorate microclimates and surface conditions for others (Billings and Mark, 1942; Whitman and Wolters, 1965).

This paper examines some relationships between microrelief and vegetation on a reclaimed coal tailings pond at Kaiser Resources Ltd., Sparwood, B.C., describes qualitative growth performance of individual species, and relates these results to reclamation practice.

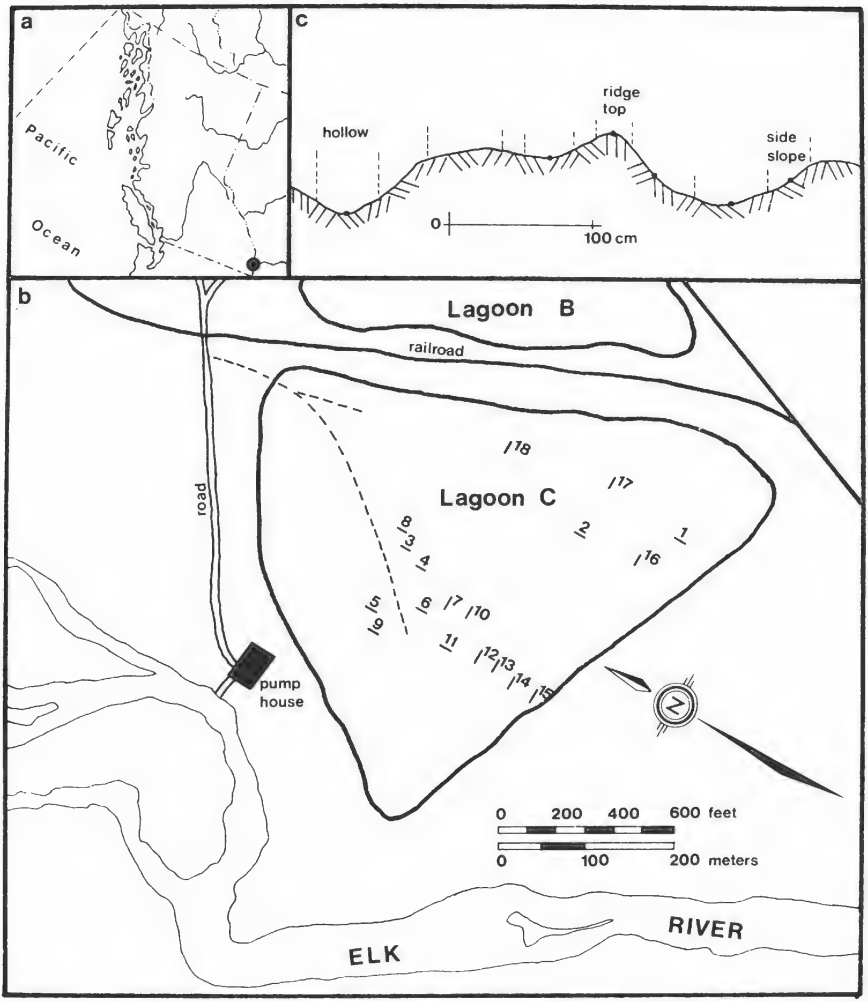


Figure 1. a) Location of study site; b) Transect locations indicated by numbers; and c) Portion of typical transect, microsites, and sample plot locations. Vertical scale exaggerated by 1/3.

**Description of Study Site**

Tailings lagoon C lies in the Elk Valley at latitude 49° 15′ and longitude 114° 41′ at elevation 1097 m a.s.l. (Fig. 1a). Local relief is moderate within mountainous terrain. The site is within the Boreal White and Black Spruce Biogeoclimatic Zone of Krajina (1965), and the Interior Subalpine Forest Region of Rowe (1972).

The climate is humid, cool temperate with a July precipitation mean of 3.6 cm and average temperature of 15.5°C. July and August appear to be months of soil moisture stress. The frost free period averages 98 days. Climatic data are summarized in Figure 2. Native soils are Dystric and Eutric Brunisols on coarse textured allu-

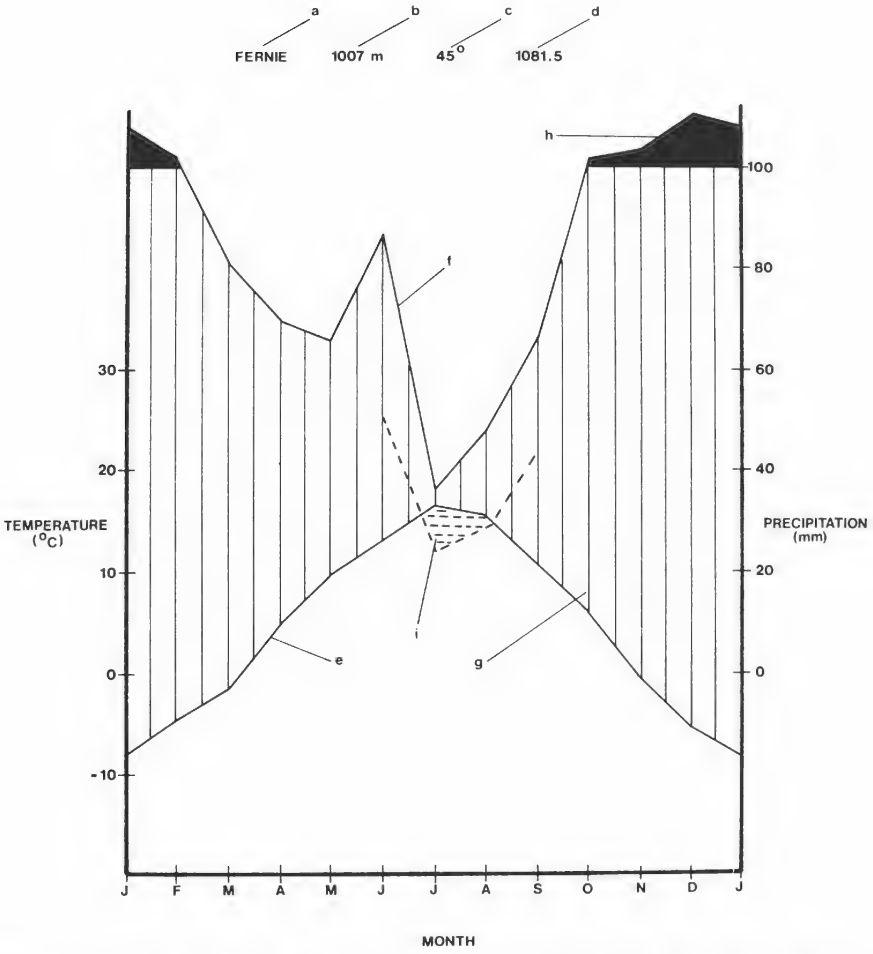


Figure 2. Climatic diagram after Walter (1973) summarizing data from nearby Fernie (Environment Canada, 1970). a = station, b = elevation in m a.s.l., c = curve of mean monthly temperature in °C, d = mean annual precipitation in mm, e = curve of mean monthly temperature, f = curve of mean monthly precipitation, g = relative humid season, h = mean monthly rain > 100 mm (black scale reduced to 1/10), i = relative period of drought (dashed scale reduced to 1/3).

vium or Luvisols over fine textured glaciolacustrine deposits (Lavkulich *et al.*, 1976). Geologically the area is in the Kootenay Formation of shales, sandstones, conglomerates, and coal. The coal is a low to medium volatile bituminous of low sulphur content and has been mined by surface and underground hydraulic methods.

Lavkulich *et al.* (1976) reports a low clay content in the tailings resulting in very low nutrient and water retention. The pH is approximately 7.0 and the sand grain size is medium, averaging .327 mm (Harrison, 1977).

Lagoon C was hydroseeded during the summer of 1976 with the following seed

Figure 3. Lagoon C showing typical surface irregularities and associated vegetation pattern.

mix at a rate of 56 kg/ha with 13:16:10 fertilizer at 168 kg/ha:20 percent creeping red fescue (*Festuca rubra* L.), 10 percent smooth brome (*Bromus inermis* Leyss.), 5 percent meadow foxtail (*Alopecurus pratensis* L.), 5 percent ryegrass (*Lolium perenne* L.), 15 percent redtop (*Agrostis alba* L.), 10 percent climax timothy (*Phleum pratense* L.), 10 percent orchardgrass (*Dactylis glomerata* L.), 10 percent alfalfa (*Medicago* spp.), 10 percent white clover (*Trifolium repens* L.), and 5 percent Canada bluegrass (*Poa compressa* L.).

Subsequent mulching with wood fiber left a vegetation cover of approximately 20 percent one year later. At seeding time the surface of lagoon C was characterized by random ridges and hollows of various sizes resulting from winter floods, snow melt, truck and scraper tracks, and animal activity (Fig. 3).

#### Methods

In mid-August 1977, five hundred sample sites were located on ridges and hollows along 18 subjectively chosen transects 0.5 m wide and averaging 10 m long. Nine transects were oriented north-south and nine east-west (Fig. 1b). Sample sites (quadrats) occurred contiguously along the transects so as to reflect changes of .5 cm or greater in relief. Sizes of quadrats therefore were variable, but all were less than or equal to 2500 $cm^2$. The microrelief was measured with a meter stick held at measured intervals along a horizontal axis. Quadrat descriptions included ocular estimates in percent of total vegetation and individual species cover. Average heights were noted and comments made on growth characters such as root development, bunching, and inflorescence development, as determined by visual inspection.

Cover data were grouped in microtopographical categories: ridge top, hollow,

north, south, east, or west facing sides of furrows (Fig. 1c). Analyses of variance were carried out on the dominant species to determine the relationship of microrelief to total vegetative cover and to cover and height of individual species as well as the relationship of individual species to each other at the microsites.

### Results and Discussion

#### Total Vegetation Cover

Species cover varied with changes in microtopography (Fig. 4) with the highest cover consistently occurring in hollows. The average total cover for hollows was significantly larger than that for ridges and west exposures. North, south, and east sides were intermediate.

Ayaad and Dix (1964) found that south facing slopes and ridges had similarly low cover. The reason for relatively high cover on south exposures here, despite the even higher temperatures (1977), may be because the hottest summer days did not occur until after the vegetation was well developed, subsequently reducing heat absorption and moisture loss at the surface.

Partial flooding of the pond during the winter was evident from large bare depressions in the center of the lagoon. In these areas it is likely that water sat for too long to permit last season's seedlings to survive and more seed to germinate. Although these barren depressions were included in the analysis, the hollows still had significantly more cover. In most areas of the lagoon, however, the vegetation seemed to benefit from the excess water retained in the hollows. Ridge sites would be expected to lose moisture fastest and to show greatest temperature rise resulting in severely impeded growth.

As some plants in exposed areas were abraded, the hollows obviously protect

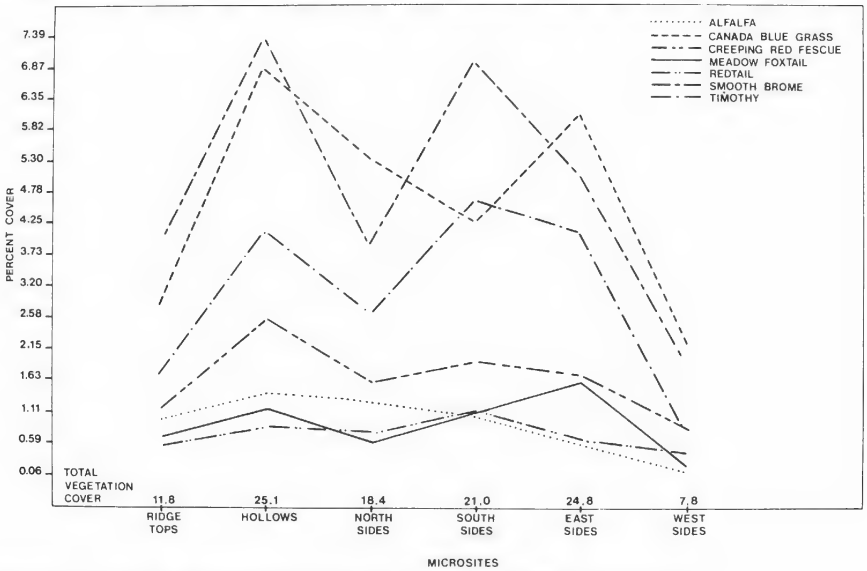


Figure 4. Average cover of the seven dominant species on different microsites.

plants from wind-blown sand. This fact would be of particular importance during seedling establishment. In some areas the vegetation had grown in the pattern of tractor treads, but wind-blown fines had since filled in the hollows. Slumping of the tailings after a combination of winter flooding and wind disturbances also appeared to reduce cover, particularly on unstable slopes.

Harrison (1977) found on Sparwood coal wastes that although southwest and southeast exposures attained approximately the same temperatures, there were substantially fewer trees on southwest exposures. He suggested that this finding may have resulted from wind. The decreased vegetation cover on west exposures of the tailings pond may be the result of wind and warmer air temperatures in the afternoon.

### Species Composition and Abundance

Of 17 species recorded in the sample plots, only seven occurred consistently. These dominants were smooth brome, Canada bluegrass, timothy, creeping red fescue, meadow foxtail, redtop, and alfalfa. Orchardgrass and white clover also were less frequent and perennial ryegrass was absent. Invading species which occurred infrequently include: crested wheatgrass (*Agropyron cristatum* L.), intermediate wheatgrass (*A. intermedium* (Host) Beauv.), pubescent wheatgrass (*A. trichophorum* (Link) Richt.). Slender wheatgrass (*A. trachycaulum* (Link) Malte.), dandelion (*Taraxacum officinale* Weber), pigweed (*Chenopodium capitatum* (L.) Asch.), squirreltail (*Sitanion hystrix* (Nutt.) Smith), and yarrow (*Achillea millefolium* (L.)).

Cover of all species showed the greatest values in hollows, the least on ridge tops and west sides, and intermediate values on north, south, and east sides ($d.f. = 5$; $F = 6.530$; $P < .001$) (Fig. 5a).

Figure 5b also shows a significant difference among cover values for some individual species ($d.f. = 6$; $F = 20.303$; $P < .001$). In the hollows smooth brome had significantly more cover than timothy, creeping red fescue, alfalfa, meadow foxtail, and redtop; so, too, Canada bluegrass had significantly greater cover than redtop and meadow foxtail. On south exposures smooth brome had significantly greater cover than Canada bluegrass, creeping red fescue, meadow foxtail, redtop, and alfalfa. On east exposures Canada bluegrass had significantly more cover than creeping red fescue, meadow foxtail, redtop, and alfalfa ($d.f. = 462$; $\alpha = .05$).

### Species Growth and Reclamation Potential

Average heights of all dominant species were not significantly different among microsites, suggesting that microtopographic variation has little influence on performance once species are established on this texturally uniform substrate.

At the time of sampling (mid-August), all plants were browning, presumably from moisture stress combined with the lateness of the season. Qualitative features of individual species are discussed below.

Smooth brome had a shallow but well developed rhizomatous root system with good erosion control capabilities. It is further adapted to tailings because it grows best on a well drained substrate and is drought resistant (Elliott and Boulton, 1970). Plants were large, with vegetative spread providing microclimate benefits that would enhance vegetation development (Ellison, 1949). Approximately 50 percent of the

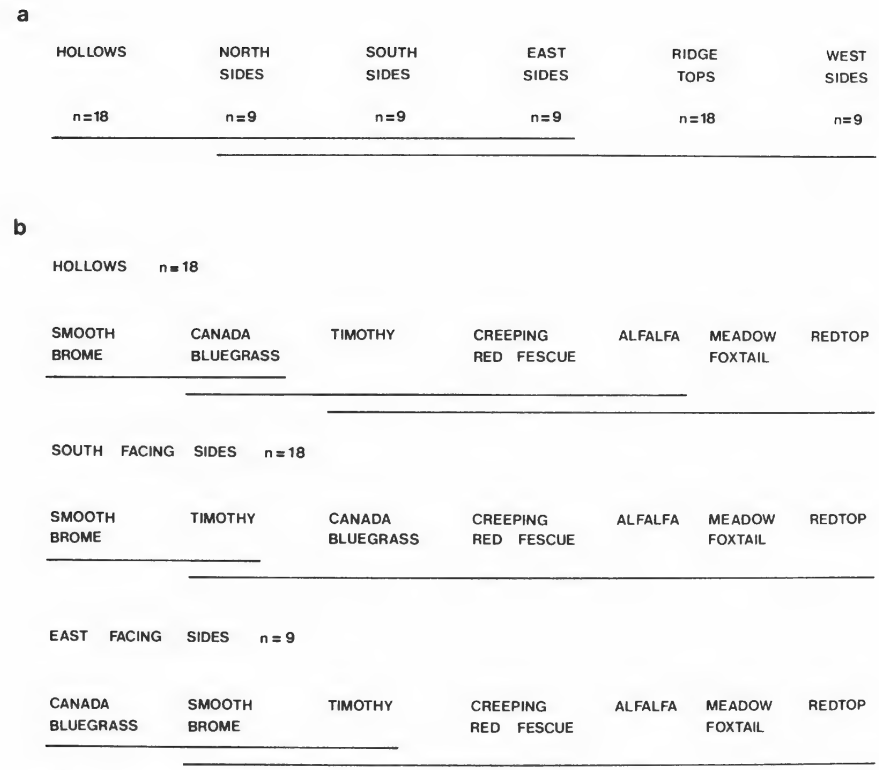


Figure 5. a) Relationship of total vegetation cover and microsites ($\alpha = .05$); and b) Relationship between species cover at the various microsites ($\alpha = .05$). Cover was significantly different between those not joined by lines.

plants had developed inflorescences. Despite its frost intolerance (Elliott and Boulton, 1970), its value at the study site is substantiated by the good growth on lagoons A and B.

Canada bluegrass had a dense, fairly deep root system with many secondary and tertiary root hairs. Approximately 40 percent of the plants had inflorescences. As a drought resistant native perennial, well suited to nutrient poor substrates (Elliott and Boulton, 1970), and with its erosion resistant turf, it is suitable for revegetation of the study site. Due to its small size and bunching habit, Canada bluegrass has less effect on the microhabitat than does smooth brome.

Timothy is a bunch grass, but little growth occurred here. The plants were usually a single stem and approximately 30 percent had inflorescences. For vigorous growth it requires ample moisture (44 to 49 cm annually, according to Elliott and Boulton, 1970). Harper *et al.* (1965) and Oomes and Elberse (1976) describe the importance of the relationship of the seed-soil interface. Timothy has small seeds, averaging 2,700,000 seeds/kg; therefore, the contact area for water uptake is large, which may aid its establishment. Such a relationship would further be improved when the surface

substrate is heterogeneous. Timothy is capable of growing on infertile soil; thus, with improved moisture conditions, its usefulness at this site would be enhanced.

Creeping red fescue did not appear to be as vigorous as the other species sampled, but Elliott and Baenziger (1973) note that a growth slowdown in summer is normal. Only 15 percent of the plants had developed inflorescences. The fibrous roots (approximately 10 cm long) did not extend as deep as might be expected (Elliott and Baenziger, 1973), although some turf was formed. It is a frost tolerant, cold resistant species which can grow on a variety of infertile soil conditions. Creeping red fescue requires less moisture than timothy, but, according to Elliott and Baenziger (1973), an ample supply is needed for truly vigorous growth. This requirement may be the factor limiting its success at the study site.

Meadow foxtail exhibited growth characteristics similar to timothy but had a lower cover percent. Due to its high moisture requirement, drought is again probably the main growth limiting factor. The species tolerates frost and flooding, enabling it to overwinter well (Elliott and Boulton, 1970). If moisture stress were to be minimal during the summer, it would be a suitable revegetation species.

Redtop performed poorly. The roots were shallow with short root stalks, and few inflorescences developed. Once established it is a drought resistant species (Elliott and Boulton, 1970), but too few became established. The value of redtop for revegetation was negligible here.

Orchardgrass is a perennial bunchgrass, but the bunching growth did not occur and inflorescences had not developed. It grew mainly in the lower depressions. It is not drought resistant, and it requires approximately 49 to 61 cm of precipitation annually as well as nitrogen fertilization to maintain a high productivity (Elliott and Boulton, 1970). These factors limit its usefulness for revegetation at the study site.

Alfalfa was stunted but had deep tap roots and good nodulation. It has some cold tolerance and drought resistance once established and is a long-lived species (McLean and Bawtree, 1971). It is probably the best suited legume for this site, as well as being valuable forage.

White clover had only established in a few locations. The roots were well nodulated but shallow; growth was not vigorous. Elliott and Boulton (1970) state that it is adversely affected by extreme changes in temperature and moisture conditions; consequently, it would be expected to do poorly at this site.

Perennial ryegrass did not occur in any of the transects. It is, however, a winter hardy, shallow rooted bunchgrass that has been successfully used for erosion control in other areas. For productive growth this species would require fertile conditions and 74 to 123 cm of moisture annually (Elliott and Boulton, 1970).

Four species of wheatgrasses occurred sporadically on the study site. Their appearance may be due to a contaminated seed lot and/or invasion from adjacent seeded areas. Crested wheatgrass was the most vigorous. This bunchgrass showed good inflorescence development and deep rooting. It adapts well to sandy soils and has been used to stabilize and revegetate many eroded prairie grassland sites (Elliott and Boulton, 1970). It has a rapid, early growth resulting in drought resistance and is therefore suitable as a reclamation species. Its low tolerance to flooding may create problems in winter at lagoon C (Knowles and Buglass, 1966).

Slender wheatgrass also had fairly good growth and inflorescences were developed.

According to McLean and Bawtree (1971), this species has a short life of two to three years; however, it develops quickly, and is most useful when sown with slower developing, longer lived plants. Its use as a reclamation species is therefore limited to the initial establishment of vegetation cover.

Intermediate wheatgrass and pubescent wheatgrass both occurred but growth was feeble. These two grasses have similar growth characteristics and are known to hybridize (Elliott and Boulton, 1970). They require medium to high fertility to develop deep roots for good sod formation, but pubescent wheatgrass is thought to be better adapted for infertile and low moisture conditions (Elliott and Boulton, 1970). In most cases, they maintain good stands where smooth brome and creeping red fescue perform well; therefore, their future use should be tested.

### Applications

Optimum microtopographic relief at this site appears to include ridges 20 to 30 cm in height at 80 to 100 cm spacing. Further controlled tests of vegetation growth on prepared hummocky surfaces of known relief would determine more specifically the most appropriate surface conditions for successful revegetation.

The choice of which of the many mechanisms to use to create microtopographic variations (Hodder, 1977; Miles *et al.*, 1973; Riley, 1973; Wolcott and Vogel, 1975) will be influenced by the actual site and economic feasibility. Large flat tailings ponds generally pose little problem for equipment manoeuvreability, but machine use on other spoil types may be largely constrained by slope conditions.

The seven species which consistently occurred over the sample site (smooth brome, Canada bluegrass, timothy, creeping red fescue, meadow foxtail, redtop, and alfalfa) are the most obvious to seed on coal tailings in this area, although redtop's low vigor may be grounds for its exclusion. The wheatgrasses (crested, intermediate, pubescent, and slender) should be tested for possible future use at the site. Ziemkiewicz (1977) suggests sowing crested wheatgrass and intermediate wheatgrass in this valley bottom as well as smooth brome, Canada bluegrass, and alfalfa. Seeding in the fall appears particularly important to ensure early seedling establishment because creeping red fescue, timothy, smooth brome, and alfalfa are slow developers (Ziemkiewicz, 1977). Fertilizer applications would probably be most effective in the spring in order to avoid winter leaching.


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# Grizzly Bear Distribution, Grand Teton National Park Area, Wyoming

**Abstract**

Thirty-two reports (1936-1979) were concentrated in northern Grand Teton National Park (GTNP) and J. D. Rockefeller Memorial Parkway (JDR). Twenty-seven reports were of single bears. Three dens were reported.

## Introduction

This paper gives information on grizzly bear (*Ursus arctos* L.) distribution in Grand Teton National Park, J. D. Rockefeller Memorial Parkway (currently administered by GTNP), and adjacent areas, demonstrating a continuity with the Yellowstone ecosystem. JDR and northern GTNP can now be valued as prehibernation and denning habitat for this threatened species.

## Methods

Information was obtained from: 1) extensive interviews with outfitters and backcountry users from 1977-79; 2) field surveys for sight and sign of bears by ourselves since 1969; and 3) files of GTNP, Bridger-Teton National Forest (BTNF), and Interagency Grizzly Bear Study Team (IGBST) flight reports.

## Results and Discussion

Figure 1 shows locations of 32 reports 1936-1979. A table giving report details is available from the authors. Reports were concentrated in JDR and along the northern shores of Jackson Lake (GTNP), with others located elsewhere along the lake and in northern GTNP. The southernmost report (#2) occurred in 1940. The concentration of reports in JDR may have been associated with the now-closed Flagg Ranch

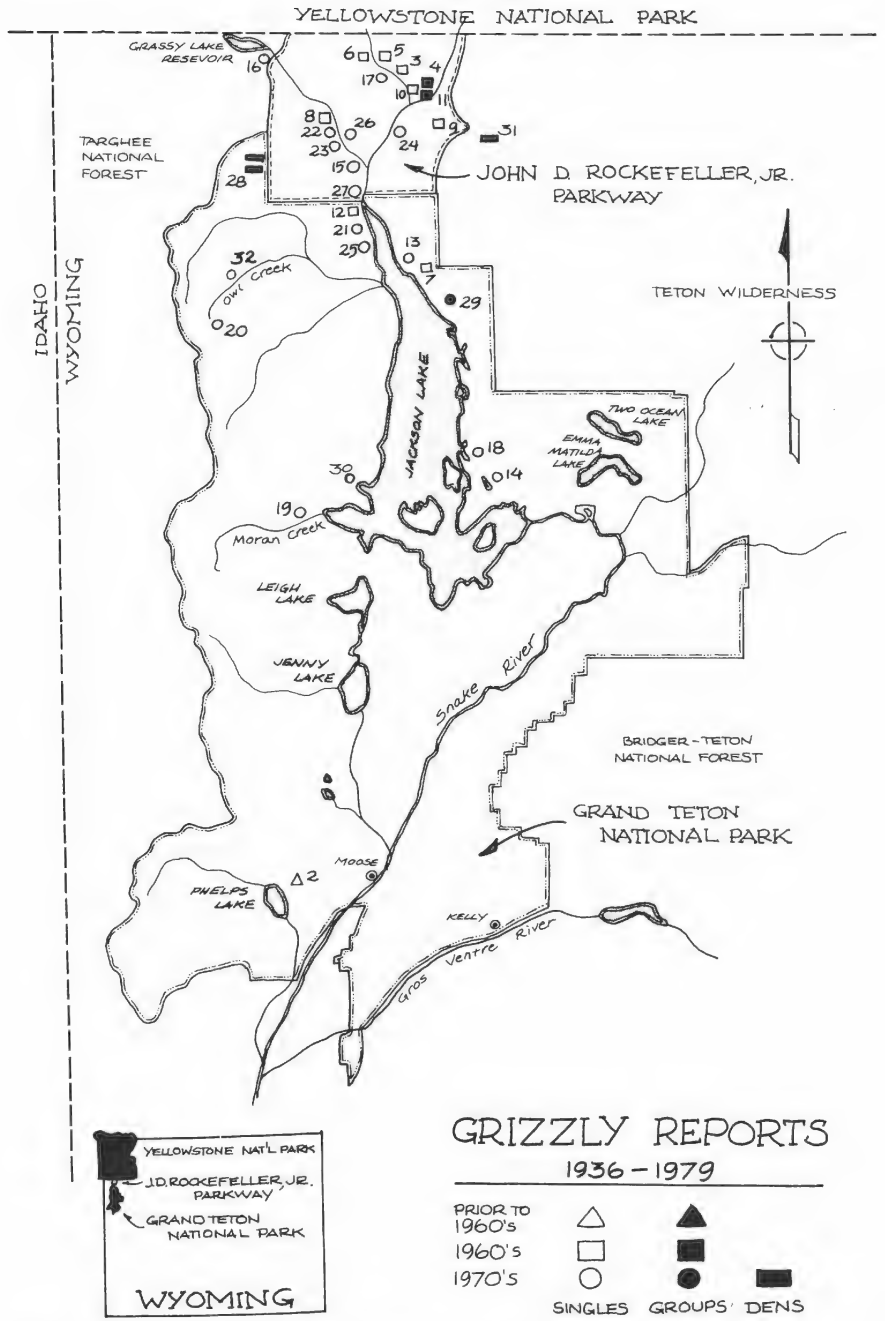


Figure 1. Locations of grizzly bear reports in Grand Teton National Park, J. D. Rockefeller Memorial Parkway, and areas immediately adjacent. (1936-1979.)

dump and nearby Snake River campground. Thirteen reports have occurred since the 1973 dump closure.

Twenty-seven reports were of single bears. Report #4 was of two adults, #29 of two subadults, and #11 of a sow with two yearlings. Other recent work by Hoak *et al.* (1980) in areas of BTNF north and east of GTNP showed higher proportions of family groups reported. A 1936 report by Murie (#1, unplotted) said he personally never saw a grizzly in GTNP, but heard of several reports. He noted that black bears were common. In a 1940 report, Gale estimated GTNP harbored 10 grizzly bears, but gave no other population data or census methods.

We compiled only two pre-1960 reports, whereas 30 were from 1968 to present. Grizzly bears have been reported each year since 1968, except 1972. 1969 yielded the highest number of reports at six. Four reports occurred in 1979. Reports spanned the months May-November, with 29 reports occurring May-September.

The three late-season reports (#27—11/77, tracks; #28—10/78, two dens; #31—11/79, den) demonstrate the importance to grizzlies of JDR and adjacent areas as denning and prehibernation habitat. The den of report #31 was confirmed by telemetry (IGBST Flight Reports, 1979). The radio-collared grizzly came from Targhee National Forest (TNF) in late September and spent the entire prehibernation in JDR, denning nearby.

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# Plant Communities and Soils of North Slopes in the Palouse Region of Eastern Washington and Northern Idaho[1]

## Abstract

Four plant community types (grass, sedge, rose, and tall shrub), at three sites on steep north slopes in the vicinity of Moscow, Idaho, were systematically sampled and analyzed. Importance values were obtained for each species in each stand based on frequency and coverage. Indices of similarity between communities from three sites were calculated to determine the discreteness and relationship of the communities. The sedge communities compared in pairs yielded indices of similarity of 68.4, 65.3, and 63.5 while those between sedge and grass communities ranged from 28.7 to 44.7. It is proposed that the community type dominated by elk sedge (*Carex geyeri*) is an undescribed topoedaphic climax plant association. The data obtained appear to warrant recognizing two previously unidentified phases of Daubenmire's *Festuca idahoensis-Symphoricarpos albus* Association, a Festuca phase and a Rosa phase.

Studies of the soil profiles of each community revealed an A2 horizon beneath the typical A and B horizons, the A2 resting on a relatively impermeable, buried B2tb horizon representing an old paleosol. During snowmelt and for several subsequent weeks, the A2 is saturated with a perched water table exhibiting a lateral water flow with consequent leaching. In none of the communities were roots seen to penetrate into the A2 horizon to any significant distance. The A2 is poorly developed in the grass stands, is closest to the soil surface in the sedge communities, and lies much deeper under the rose and tall shrub communities. The rhizosphere water becomes depleted earliest in the grass stands; in the sedge communities, it is present in above optimal amounts far into the spring. This condition appears to be unfavorable for many plant species typical of the Palouse prairie, and it allows elk sedge to assume dominance. The thick A1 and upper B horizons above the A2, low in clay and with an adequate supply of available soil moisture throughout the growing season, create optimum conditions for the rose and tall shrub communities.

The depth to the A2 horizon and the subtending paleosolic B2tb below the surface is the most important extrinsic factor determining the distribution of grass, sedge, and shrub communities on steep north slopes in the study area.

## Introduction

The occurrence of two forest plant species, ladyslipper orchid (*Cypripedium montanum* Dougl. ex. Lindl.) and a dwarf huckleberry (*Vaccinium caespitosum* Michx.), on an

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undisturbed steep north slope in the Palouse prairie region near Moscow, Idaho, was the original impetus for undertaking this study. A reconnaisance of this slope (Site I) revealed three rather well defined plant communities and a possible fourth in an ostensibly uniform macrohabitat.

It was postulated that the presence and position of the four plant communities were related to soil moisture. Furthermore, it was assumed that if these communities were discrete and climax, they might be found in similar habitats elsewhere in the region. Accordingly, a search was made for other steep north exposures which had not been cultivated, grazed, or burned in recent decades. Two additional undisturbed north slopes were located which supported the same four communities noted on Site I. One of these (Site II) is near Moscow and the other (Site III) is located some 20 km southwest of Moscow near Colton, Washington.

All three sites are characterized by micro-topographic irregularities to which the distribution of the plant communities correspond rather closely. The question investigated was whether these irregularities and their associated environmental factors could account for the four communities and for their repetition on the three sites.

The complex, multifaceted process leading to the formation of the Palouse hills has produced an unusual soil profile and a related unique soil moisture regime. For example, Rieger and Smith (1955) and Garber (1965) have described lateral water movement through the soil on north slopes in the Palouse area that resulted in perched water tables. These conditions prevail primarily during the first part of the growing season when snowmelt and rainfall reach their peaks.

In a study of soil drought and its influence in the distribution of vegetation in the northern Rocky Mountains, McMinn (1952) suggested a relationship between moisture and the distribution of grass and shrub communities on the Palouse slopes. His studies were involved with the depletion of growth water in the soil during the latter part of the growing season. For example, he found that the soils in the grass communities were the first to show moisture deficiency. He contended that the onset of soil drought was a major factor in the formation of distinct communities, e.g., the grasses growing in areas of earliest moisture depletion, and the shrubs occupying the parts of the slope that retained moisture longest defined these communities. He postulated that seedlings from the shrub communities could not become established in grassy areas because the rate of root growth of these seedlings was outstripped by the loss of adequate moisture.

The authors of this paper also postulate that the soil moisture regime is the factor maintaining these communities; but it is our hypothesis that the amount of soil moisture and the related soil oxygen content during the first part of the growing season is most important.

The objectives of the study, then, were to determine if the plant communities are discrete and climax, and what factors control their presence and distribution on these north slopes. Their structure and composition were studied and compared with each other. Their soils were examined for physical and chemical properties, and special attention was given to determining soil moisture by horizons.

#### Descriptions of Sites

Site I, owned by Mrs. Marketta Buckler, located approximately 2.5 km west of Moscow,

Idaho, in Whitman County, Washington, in Sec. 5, T 14 N, R 46 E at Lat. 46° 43′ N, comprises about one hectare and has a slope of 56 percent in the upper one third of its aspect. The mean elevation is approximately 840 m above sea level.

Site II, owned by Christine Cameron, located 4 km southeast of Moscow, Idaho, Latah County, in Sec. 20, T 9 N, R 5 W at Lat. 46° 42′ N, comprises about four hectares and has a mean elevation of approximately 841 m.

Site III is a part of a Palouse prairie remnant in Whitman County, Washington, owned and preserved by Washington State University. It is located 7 km northwest of Colton, Washington, in Sec. 25, T 13 N, R 44 E at Lat. 46° 35′ N with a mean elevation of about 836 m.

The Palouse region of eastern Washington and adjacent Idaho contains a series of loess deposits, the Palouse Formation, that overlie the Columbia River basalts. The eastern sector of the Palouse Province is characterized by hilly topography which is the result of the action of several forces: 1) the dissection of the basalts prior to loess deposition; 2) the prevailing southwesterly winds, which have been the deposition agent; 3) the differential erosion of the loess by precipitation; 4) the headward erosion by large amounts of snow which accumulate on these north slopes during the winter months; and 5) lateral flow of soil moisture over a restricting subsoil with subsequent mass movement; e.g., slumping during the wet season. As a result of the interplay of these factors, the hills have a dune-like form with a SW/NE alignment.

The climate of the region is Mediterranean with cool, moist winters and warm, dry summers. The native vegetation of the eastern portion of the Palouse is primarily meadow-steppe, with the exception of shrubby areas on the north slopes and stream bottoms. A large portion of the precipitation falls in the form of snow. In the Moscow area the average annual snowfall over a 28-year period was 140 cm, 64 percent of which fell between 1 January and 30 April (Climatological Data, Idaho Section, 1946-1974). Rockie (1950) points out that the accumulation of great depths of snow on the lee slopes is favored by the winter snowfall rate reaching its maximum during the same period that the prevailing southwesterly winds attain their average peak velocities. The relatively long retention of the drifts is augmented by the low angle of incidence of the sun at the high latitude of the Palouse region. Rockie also found that steep north exposures have the equivalent of 150-200 cm of annual precipitation compared to 52-60 cm (Klages, 1942) for level areas in the same region.

The uniformity of the loess material deposited is reflected in the similarity in soils that occur throughout the region. Thatuna silt loam soils have developed on the lee slopes; i.e., the north and east slopes—and they show the strongest degree of horizon development to be found in the study. These Thatuna soils are characterized by a thick A1 and a prominent A2 over a strongly developed B2tb horizon (Lotspeich and Smith, 1953).

The loess has been deposited in successive layers since early Pleistocene times, and paleosols have developed in the earlier depositions. These paleosols are characterized by large amounts of silt, moderately high quantities of accumulated clay, and high bulk densities which render them very slowly permeable to water, resulting in perched water tables in the spring. This perched ground water tends to move laterally along the upper surfaces of the paleosol in sufficient amounts to have created a leached zone, or A2 horizon.

During periods of saturation, the eluviated material of the A2 horizon becomes fluid and acts as a shear plane. The steepness of the slope contributes to its instability, causing slumping and headward erosion. The result of such movement is an arcuate shape on the north slopes and a low undulating relief (Garber, 1965).

## Methods and Procedures

### Soil Factors

Soil moisture data were taken every two weeks during three successive growing seasons at 15 cm intervals to a depth of 150 cm in each of the four communities at Sites I and II. This pattern was followed also at Site III on 22 April and 19 May 1978 in order to obtain soil moisture percentages at that location. During the first growing season, soil moisture determinations were made by gravimetric procedures. During the second and third years, these data were obtained by a Troxler moisture neutron probe. At the end of the third season, soil pits were dug in each of the four communities at Sites I and II, and soil descriptions were made by standard procedures (Soil Survey Staff, 1975). Bulk and clod samples were collected by horizon, air-dried, and passed through a 2 mm sieve for laboratory analyses. They were analyzed using standard methods (Soil Conservation Service, 1972) in the Soil Characterization Laboratory at the University of Idaho.

### Vegetation Sampling

Macroplots were laid out in each community in such a manner as to sample the entire community yet avoid ecotones and still leave no substantial part of the community unsampled. In the grass and sedge communities 2 m x 2.5 m macroplots were employed with 5 m x 5 m used in the shrub communities. Each macroplot was divided into 50 microplots, 2 dm x 5 dm in the grass and sedge plots, and 0.5 m x 1.0 m in the shrub communities. The long axis in each case was perpendicular to the contour of the slope. We employed a minimum of 40 microplots chosen randomly from the macroplots in the grass and sedge communities; the exception to this technique was Sedge II in which, because of its small size, only 20 microplots were used. All plants in each microplot were determined to species by authority of *Flora of the Pacific Northwest* (Hitchcock and Cronquist, 1973). The crown coverage of each species was estimated and placed in one of five cover classes as follows:

| Cover Class Number | Range of Coverage | Midpoint for Each Cover Class Used for Average |
|---|---|---|
| 1 | 5% or less | 3% |
| 2 | 6% to 25% | 15% |
| 3 | 26% to 50% | 38% |
| 4 | 51% to 75% | 68% |
| 5 | 76% to 100% | 88% |

The mean coverage and the frequency were computed for each species: these values were converted to relative coverage and relative frequency, respectively, then summed to give the importance value (I.V.). Density of species was not determined; thus, only two of the three parameters proposed by Curtis and McIntosh (1951) were employed. The I.V.s were used as a measure of dominance.

A valid index of similarity (I.S.) was needed to determine the resemblance of communities and to test for their discreteness. Acting on Gleason's suggestion, as discussed by Bray and Curtis (1957), that Jaccard's coefficient of community is more meaningful if quantitative measures of species rather than mere species lists are used, the I.V.s of species were employed to determine an index of similarity between communities within one site, and between similar communities at different sites. The following formula was used: $\text{I.S.} = \frac{2w}{a+b} \times 100$ in which a = the sum of the I.V.s of all the species in one stand, b = the similar sum for the second stand, and w = the sum of the lower of each pair of I.V.s for those species which are common to both stands.

**Results and Conclusions**

Soils

Soil profiles, physical properties, and the subsequent data from laboratory analyses of these soils for each plant community show many similarities as well as important differences among soils. Generally, the soils appear to represent a continuum with closely related components that have characteristic topographic positions and chemical and physical soil properties that relate to specific plant communities.

The landform is north to northeast facing and crescent shaped. It has a very steep 40 to 50 percent uniform upper slope, and the middle to lower slopes (15 to 40 percent) consist of small ridges and swales perpendicular to the slope.

Bands of varying types of vegetation appear to be correlated with the crests and depressions of this undulating topography and to the steeper positions on the headward slope. The grass and sedge communities occur on those areas that presumably have not been affected by this slumping, or where mass wastage has thinned the surface soil. The grass stands are confined to areas of higher relief and the sedge to the depressed areas. The rose and tall shrub communities occur on soils having thick A and B horizons overlying the A2 and the B2tb of the paleosols. They are present on slump areas and upper slopes.

At Site II, measured depths of snow were 60 cm or less for the grass, 90 cm to 150 cm for the sedge and rose, and over 300 cm for the tall shrub.

Soil moisture data given in Table 1 show that in the sedge sites the soils are saturated closest to the surface, grass soils are less saturated and the moisture is depleted earlier in the season. Rose and tall shrub sites show saturation at greater depths and a thicker non-saturated surface soil.

Soil pit studies revealed that there was minimal root penetration into the A2 horizon in all the plant communities.

The soil horizon symbol is by definition an interpretation of the genesis of the soil and its horizon properties. The horizonation sequence for all seven sample areas studied as generalized in Figure 1 is A1, A3, B1, B2t, A2, and B2tb. The similarity in horizonation shows these soils are all similar with major differences in thickness and depth of horizons, degree of development of the A2, and differences in organic matter accumulation. Each soil has two horizon sequences. The upper A and B se-

TABLE 1. Percent soil moisture by volume for three plant communities at Site II and one plant community at Site I during the growing season of 1967.

| SOIL DEPTH IN CM | GRASS COM. SITE II | | | | SEDGE COM. SITE I | | | | ROSE COM. SITE II | | | | TALL SH. COM. SITE II | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | JE | JY | AU | M | JE | JY* | AU* | M | JE | JY | AU | M | JE | JY | AU |
| 15.0 | 26.7 | 30.1 | 15.2 | 11.7 | 46.9 | 38.9 | 22.0 | 13.2 | 40.6 | 39.2 | 19.8 | 17.3 | 43.2 | 42.6 | 26.2 | 21.8 |
| 30.0 | 34.4 | 28.4 | 15.6 | 13.6 | 42.0 | 34.1 | 24.4 | 14.0 | 41.4 | 41.6 | 20.4 | 17.2 | 44.9 | 46.6 | 25.5 | 21.5 |
| 45.0 | 38.4 | 33.2 | 22.3 | 15.7 | 45.4 | 34.6 | 26.3 | 13.0 | 40.0 | 31.2 | 22.2 | 17.3 | — | 36.4 | 25.0 | 21.3 |
| 60.0 | 37.9 | 35.5 | 29.2 | 16.0 | 44.2 | 37.2 | 27.3 | 12.0 | 37.5 | 34.9 | 27.6 | 18.3 | 40.1 | 36.9 | 28.7 | 24.7 |
| 75.0 | 37.0 | 35.8 | 27.5 | 18.6 | 37.6 | 35.8 | 26.4 | 21.5 | 41.7 | 35.2 | 30.0 | 20.5 | 37.6 | 35.1 | 28.6 | 24.6 |
| 90.0 | 36.3 | 37.8 | 27.7 | 17.3 | 47.0 | 33.7 | 43.5 | 32.5 | 42.9 | 46.5 | 33.1 | 15.5 | 32.8 | 36.4 | 31.4 | 25.4 |
| 105.0 | 34.7 | 42.1 | 36.0 | 39.5 | 45.5 | 40.5 | 56.8 | 34.5 | 43.8 | 40.7 | 39.9 | 25.8 | 21.9 | 37.4 | 35.2 | 29.8 |
| 120.0 | 46.7 | 39.7 | 42.1 | 42.5 | 41.9 | 40.7 | 60.0 | 35.0 | — | 46.6 | 43.2 | 40.1 | 23.6 | 52.3 | 58.7 | 34.6 |
| 135.0 | 43.6 | 41.9 | 38.3 | 39.9 | 41.0 | 40.1 | — | — | 49.6 | 42.9 | 43.8 | 40.5 | 25.9 | 46.5 | 52.5 | 37.8 |
| 150.0 | 41.1 | 42.0 | 39.9 | 42.2 | 37.8 | 41.6 | — | — | 44.2 | 48.2 | 43.2 | 25.7 | 23.0 | 57.7 | 52.2 | 39.0 |

*Data from 1969

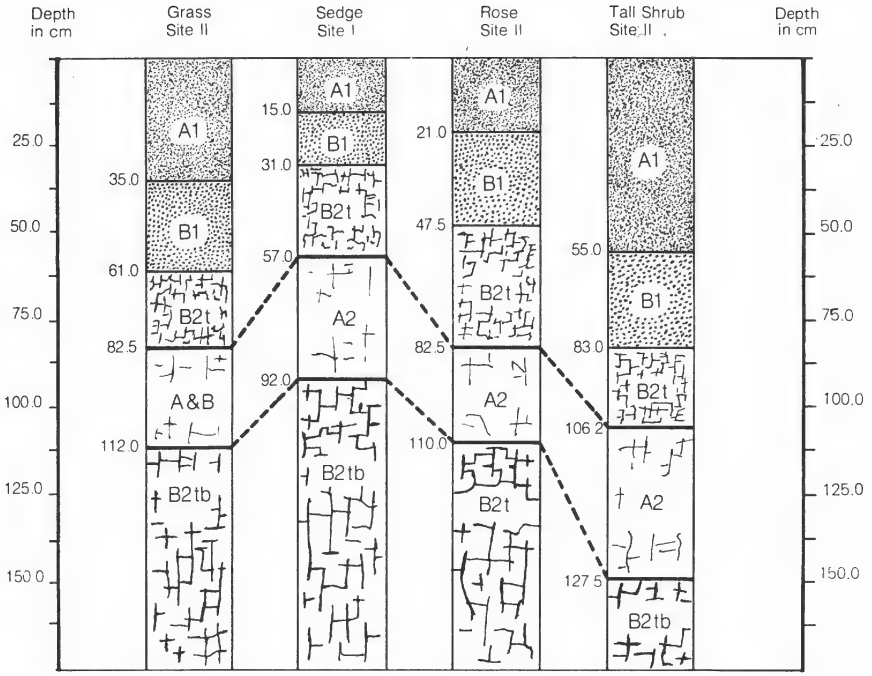


Figure 1. Soil horizon sequence emphasizing position of A2 horizon-zone of water movement.

quence is developed in a younger loess deposit which buried an older soil that partially represents the lower or buried A and B sequence. A study of the soils in the Palouse region tells us that the A2 is a product of lateral water movement. It occurs in soils in areas or positions in the landscape where there is sufficient water to percolate deep enough to be intercepted by a restricting horizon which in these soils is the B2tb. Therefore, the A was not present when the soil was buried, but was formed later in the original surface horizons of the buried soil.

The laboratory data (Table 2) show that the A2 has less clay, lower CEC, and less organic matter than horizons above or below. These properties and lighter color values verify the degree of development of the A2 horizon.

The organic matter or organic carbon must come from plant material grown on the soil. The amount of organic matter accumulation depends on the kind of plant community and the moisture, as modified by the effect of topography. The total accumulation of organic matter in all horizons above the A2 is given in Table 3. The data show that these soils have a thick, dark surface high in organic matter down to the A2 horizon. There is a trend for increasing organic matter from grass to tall shrub. The other physical and chemical properties are similar for each soil.

### The Plant Communities

Noteworthy are the relatively sharp ecotones separating the four community types in the study. This is not a new observation in the steppe area of southeastern Washington.

TABLE 2. The physical analyses and chemical characterization of the profile Thatuna silt loam 69-WA-3806.

| Sample No. | Horizon | Depth | Bulk Density | Particle Size Distribution Sand | Silt | Clay | Textural class |
|---|---|---|---|---|---|---|---|
| | | cm | g/cc | | % | | |
| 1 | A11 | 0-10 | 1.28 | 7.34 | 69.52 | 23.14 | Silt loam |
| 2 | A12 | 10-18 | 1.31 | 9.64 | 68.33 | 22.03 | Silt loam |
| 3 | B1 | 18-35 | 1.31 | 1.09 | 74.36 | 24.54 | Silt loam |
| 4 | B2t | 35-63 | 1.41 | 6.98 | 69.15 | 23.87 | Silt loam |
| 5 | A&B | 63-73 | 1.61 | 7.97 | 75.19 | 16.84 | Silt loam |
| 6 | A2 | 73-83 | 1.70 | 8.07 | 78.81 | 13.12 | Silt loam |
| 7 | Bb&A | 83-95 | 1.70 | 7.02 | 64.56 | 28.42 | Silty clay loam |
| 8 | B21tb | 95-105 | 1.79 | 5.77 | 57.07 | 37.16 | Silty clay loam |
| 9 | B22tb | 105-150 | 1.82 | 5.58 | 57.00 | 37.43 | Silty clay loam |

| Sample No. | Paste pH | Exchangeable Ions Ca | Mg | Na | K | H | CEC | Base Sat. | OM | N |
|---|---|---|---|---|---|---|---|---|---|---|
| | | meq/100 g soil | | | | | | % | % | % |
| 1 | 5.95 | 9.38 | 4.13 | 0.10 | 3.50 | 7.18 | 23.00 | 70 | 5.54 | 0.31 |
| 2 | 6.10 | 10.00 | 4.88 | 0.10 | 3.40 | 7.63 | 25.91 | 71 | 9.06 | 0.40 |
| 3 | 5.98 | 7.50 | 3.75 | 0.10 | 2.00 | 6.88 | 20.18 | 66 | 3.94 | 0.24 |
| 4 | 5.90 | 6.88 | 3.75 | 0.15 | 1.50 | 6.27 | 18.09 | 66 | 2.24 | 0.15 |
| 5 | 6.00 | 5.00 | 3.25 | 0.18 | 0.70 | 4.00 | 12.73 | 70 | 1.07 | 0.07 |
| 6 | 5.35 | 5.00 | 2.50 | 0.18 | 0.34 | 3.02 | 10.91 | 73 | 0.57 | 0.04 |
| 7 | 5.85 | 7.50 | 5.50 | 0.28 | 0.62 | 4.38 | 19.18 | 76 | 0.67 | 0.05 |
| 8 | 5.75 | 10.00 | 6.88 | 0.40 | 0.99 | 6.04 | 25.91 | 75 | 0.69 | 0.05 |
| 9 | 5.65 | 13.13 | 7.75 | 0.43 | 1.25 | 7.60 | 27.36 | 75 | 0.40 | 0.03 |

TABLE 3. The average total organic matter accumulation in the rhizosphere in each plant community.

| Community | Grass | Sedge | Rose | Tall shrub |
|---|---|---|---|---|
| Percent Organic Matter | 17.3 | 19.8 | 24.9 | 25.9 |

Daubenmire (1942) noted that a slight difference in soil depth and a minor increase in soil moisture brought about by dust and snow accumulation caused by a 3-strand barbed wire fence across a *Festuca-Agropyron* Association resulted in a *Rosa-Symphoricarpos* Association growing along the fence.

*The Sedge Communities.* The sedge stands from Sites I, II, and III are comprised of 24, 22, and 23 species of angiosperms, respectively; they have a total of 33 species, 31 of which are indigenes. Elk sedge (*Carex geyeri*), as noted in Table 4, has frequencies and coverages of 100 and 72 percent, 95 and 52.3 percent, and 100 and 74.4 percent, respectively, in Sites I, II, and III.

The occurrence of only two adventive species—*Poa pratensis* in Site I and a small species of *Bromus* in Site III—strongly suggests that sedge stands are closed communities. The high indices of similarity (I.S.s) between the three sedge stands as shown in Table 5 (68.4, 65.3, and 63.5) support the contention that these three stands belong to the same community type. By contrast, the indices of similarity between Grass II and Sedges I, II, and III (see Table 5, comparisons 10, 6, and 7) are 28.7, 44.7, and 38.8, respectively, with a mean of 37.4.

A significant difference between Grass II stand and the sedge communities is revealed by noting the dominant and some of the more important subordinant species

which characterize the stands. The obvious dominance of *Carex geyeri* in Sedge I, II, and III with I.V.s of 68.5, 63.5, and 87.2, respectively, is in sharp contrast to its I.V. of only 7.8 in Grass II (Table 6). Idaho fescue (*Festuca idahoensis*) is clearly the major dominant in Grass II, with an I.V. of 36.3. It is absent from Sedge III and is

TABLE 4. Frequencies, coverages, and importance value of species in the sedge communities in sites I, II, and III (frequencies and coverages were converted to relative frequencies and relative coverages, respectively, to obtain important values).

| | Frequency Site | | | Coverage Site | | | Importance Value Site | | |
|---|---|---|---|---|---|---|---|---|---|
| | I | II | III | I | II | III | I | II | III |
| **Carex geyeri** | 100.0 | 95.0 | 100.0 | 72.0 | 52.3 | 74.4 | 68.5 | 63.5 | 87.2 |
| **Fragaria virginiana** | 80.0 | 65.0 | | 8.7 | 4.4 | | 18.5 | 12.9 | |
| **Vaccinium caespitosum** | 75.0 | | | 17.8 | | | 24.5 | | |
| **Aster** sp. | | 80.0 | | | 7.8 | | | 18.3 | |
| **Symphoricarpos albus** | 77.5 | 45.0 | 70.0 | 8.5 | 3.2 | 8.0 | 18.0 | 4.1 | 18.1 |
| **Gentiana affinis** | 52.5 | 45.0 | 14.0 | 3.1 | 2.0 | 0.7 | 10.2 | 7.9 | 2.9 |
| **Viola adunca** | 50.0 | 90.0 | 28.0 | 2.1 | 3.1 | 1.1 | 9.0 | 15.3 | 5.6 |
| **Potentilla gracilis** var. **flabelliformis** | 32.5 | 50.0 | 42.0 | 4.3 | 4.5 | 2.7 | 8.1 | 11.1 | 9.4 |
| **Galium boreale** | 30.0 | 45.0 | 58.0 | 1.2 | 2.0 | 2.7 | 5.4 | 7.9 | 12.6 |
| **Geranium viscosissimum** | 25.0 | 25.0 | 20.0 | 2.6 | 2.0 | 1.1 | 5.4 | 5.2 | 4.3 |
| **Rosa nutkana** | 22.5 | 5.0 | 10.0 | 2.8 | 0.2 | 0.5 | 5.4 | 0.8 | 2.1 |
| **Iris missouriensis** | 22.5 | | 38.0 | 1.0 | | 1.1 | 4.0 | | 7.3 |
| **Heuchera cylindrica** | 20.0 | 20.0 | 4.0 | 1.8 | 1.8 | 0.4 | 4.3 | 4.4 | 1.0 |
| **Amelanchier alnifolia** | 15.00 | 5.0 | 8.0 | 2.8 | 0.2 | 1.0 | 4.3 | 0.8 | 2.2 |
| **Wyethia amplexicaulis** | 10.0 | | | 3.5 | | | 4.1 | | |
| **Lupinus sericeus** | 10.0 | 5.0 | 14.0 | 0.6 | 0.8 | 1.1 | 1.9 | 1.4 | 3.4 |
| **Hypericum perforatum** | 10.0 | | | 0.6 | | | | | |
| **Geum triflorum** | 10.0 | 30.0 | 56.0 | 0.3 | 2.1 | 4.3 | 1.7 | 6.1 | 13.3 |
| **Calamagrostis rubescens** | 5.0 | 60.0 | | 0.2 | 5.4 | | 0.9 | 13.3 | |
| **Balsamorhiza sagittata** | | 5.0 | | | 0.2 | | | 0.8 | |
| **Agropyron spicatum** | | 5.0 | | | 0.2 | | | 0.8 | |
| **Sisyrinchium inflatum** | | 5.0 | | | 0.2 | | | 0.8 | |
| **Poa pratensis** | 2.5 | | 4.0 | 0.1 | | 0.1 | 0.4 | | 0.8 |
| **Potentilla arguta** | 2.5 | | 16.0 | 0.4 | | 1.4 | 0.6 | | 4.0 |
| **Festuca idahoensis** | 2.5 | 5.0 | | 0.4 | 0.6 | | 0.6 | 0.8 | |
| **Achillea millefolium** ssp. **lanulosa** | 2.5 | 10.0 | 32.0 | 0.1 | 6.3 | 1.0 | 0.4 | 7.5 | 6.1 |
| **Spiraea betulifolia** var. **lucida** | 2.5 | 15.0 | 4.0 | 0.1 | 1.1 | 0.1 | 0.6 | 3.0 | 0.8 |
| **Hieracium albertinum** | 2.5 | 35.0 | 34.0 | 0.1 | 4.0 | 1.5 | 0.4 | 8.6 | 7.0 |
| **Besseya rubra** | | | 32.0 | | | 0.1 | | | 6.1 |
| **Sidalcea oregana** | | | 12.0 | | | 0.4 | | | 2.3 |
| **Silene oregana** | | | 8.0 | | | 0.2 | | | 1.5 |
| **Castilleja lutescens** | | | 4.0 | | | 0.1 | | | 0.8 |
| **Bromus** sp. | | | 4.0 | | | 0.1 | | | 0.8 |

TABLE 5. Indices of similarity between various communities by sites.

| Comparison | Community and Site | Community and Site | Index of Similarity |
|---|---|---|---|
| 1 | Sedge I | with Sedge II | 68.4 |
| 2 | Sedge II | with Sedge III | 65.3 |
| 3 | Sedge I | with Sedge III | 63.4 |
| 4 | Tall shrub II | with Rose II | 59.0 |
| 5 | Grass II | with Rose II | 46.5 |
| 6 | Grass II | with Sedge II | 44.7 |
| 7 | Grass II | with Sedge III | 38.8 |
| 8 | Grass II | with Tall shrub II | 36.9 |
| 9 | Tall shrub II | with Sedge II | 36.6 |
| 10 | Grass II | with Sedge I | 28.7 |

TABLE 6. A comparison of importance values of the dominant species and of some of the more important subordinant species in Grass II, Sedge I, Sedge II, and Sedge III stands.

| Species | Importance Value | | | |
|---|---|---|---|---|
| | Grass II | Sedge I | Sedge II | Sedge III |
| **Carex geyeri** | 7.8 | 68.5 | 63.5 | 87.2 |
| **Festuca idahoensis** | 36.3 | 0.6 | 0.8 | |
| **Vaccinium caespitosum** | | 24.5 | | |
| **Fragaria virginiana** | 5.6 | 18.5 | 12.9 | |
| **Symphoricarpos albus** | 7.3 | 18.0 | 9.1 | 18.1 |
| **Viola adunca** | 3.9 | 9.4 | 15.3 | 5.6 |
| **Potentilla gracilis** var. **flabelliformis** | 14.7 | 8.0 | 11.1 | 9.4 |
| **Achillea millefolium** ssp. **lanulosa** | 12.5 | 0.4 | 7.5 | 6.1 |

represented in Sedge I and II by I.V.s of only 0.6 and 0.8, respectively. Other species showing notable differences in I.V.s between grass and sedge communities are snowberry (*Symphoricarpos albus*), strawberry (*Fragaria virginiana*), yarrow (*Achillea millefolium* ssp. *lanulosa*), and *Viola adunca.* Grass II has a total of 48 species of angiosperms (43 indigenes and 5 adventives), only 22 of which are shared by the sedge communities.

The finding of an abundance of young elk sedge shoots in the sedge community at Site I suggests the permanency of this species. The sedge stands were always found associated with soil profiles having shallow A1 and B horizons that rest on an A2 over a restrictive B2tb horizon. An abundant supply of moisture to the root zone (horizons A1, B1, and B2t) keeps it near saturation far into the growing season. It would appear that elk sedge is better adapted to a saturated rhizosphere with a possible oxygen deficit than are most other typical Palouse area plant species. Thus, the sedge replaces them in this unique edaphic habitat. The low species numbers in the sedge communities at the three sites support these conclusions.

In view of the data presented, we propose that the stands in this study dominated by *Carex geyeri* represent an undescribed topoedaphic climax association for the Palouse region of southeastern Washington and adjacent Idaho. It is a matter of conjecture how many more examples of this association existed under pristine conditions but have disappeared as a result of cultivation. On a hill near Pullman, Washington, Weaver (1914) found *carex geyeri* represented on 67 percent of the plots taken on northeast slopes with six "bunches" of sedge per square meter. On the southwest exposure, this species occurred on only 3 percent of the quadrats.

*The Grass Communities.* Data from the community at Site I originally thought to comprise a discrete grass community revealed that 15 percent of its plant species are adventives and that Idaho fescue is only a subordinate species. It was concluded that the area is not a natural community and its data were not used in obtaining indices of similarity.

The grass stand at Site II is dominated by Idaho fescue with a frequency of 97.5 percent, a coverage of 25.5 percent, and an I.V. of 36.3 (Table 7). Ranking second and third in importance values are *Potentilla gracilis* var. *flabelliformis* with a figure of 14.7 and *Achillea millefolium* ssp. *lanulosa* at 12.5. A total of 48 species were found in the sample plots at this site.

Attention was called earlier to Table 5 which showed the low I.S.s between Grass II and the three sedge stands. Relatively low I.S.s should be noted also between Grass

TABLE 7. Frequencies, coverages, relative frequencies, relative coverages and importance values of the vascular plant species in the sedge community of Site I and the grass community of Site II.

| Species | Frequency | | Coverage | | Rel. Freq. | | Rel. Cov. | | Imp. Value | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Gr.C. | Se.C. | Gr.C | Se.C. | Gr.C. | Se.C. | Gr.C. | Se.C. | Gr.C. | Se.C. |
| **Carex geyeri** | 37.5 | 100.0 | 3.8 | 72.0 | 3.9 | 15.1 | 3.9 | 53.4 | 7.8 | 68.5 |
| **Festuca idahoensis** | 97.5 | 2.5 | 25.5 | 0.4 | 10.1 | 0.4 | 26.0 | 0.3 | 36.3 | 0.7 |
| **Fragaria virginiana** | 27.5 | 80.0 | 2.6 | 8.7 | 2.9 | 12.1 | 2.7 | 6.4 | 5.5 | 18.5 |
| **Symphoricarpos albus** | 45.0 | 77.5 | 2.5 | 8.5 | 4.7 | 11.7 | 2.6 | 6.3 | 7.2 | 18.0 |
| **Vaccinium caespitosum** | | 75.0 | | 17.8 | | 11.3 | | 13.2 | | 24.5 |
| **Achillea millefolium** subsp. **lanulosa** | 70.0 | 2.5 | 5.1 | 0.1 | 7.3 | 0.4 | 5.2 | 0.1 | 12.5 | 0.4 |
| **Potentilla gracilis** var. **ilabelliformis** | 62.5 | 32.5 | 8.0 | 4.3 | 6.5 | 4.9 | 8.2 | 3.2 | 14.7 | 8.1 |
| **Gentiana affinis** | 7.5 | 52.5 | 0.5 | 3.7 | 0.8 | 7.9 | 0.5 | 2.3 | 1.3 | 10.2 |
| **Viola adunca** | 20.0 | 50.0 | 1.8 | 2.1 | 2.9 | 7.5 | 1.8 | 1.6 | 3.9 | 9.1 |
| **Lomatium triternatum** | 50.0 | | 3.9 | | 5.2 | | 3.9 | | 9.2 | |
| **Collinsia parviflora** | 50.0 | | 2.7 | | 5.2 | | 2.8 | | 7.9 | |
| **Aster** sp. | 42.5 | | 3.1 | | 4.4 | | 3.1 | | 7.5 | |
| **Calamagrostis rubescens** | 37.5 | 5.0 | 3.8 | 0.2 | 3.9 | 0.8 | 3.9 | 0.1 | 7.8 | 0.9 |
| **Galium boreale** | 32.5 | 30.0 | 1.9 | 1.2 | 3.4 | 4.5 | 1.9 | 0.9 | 5.3 | 5.4 |
| **Geum triflorum** | 30.0 | 10.0 | 3.3 | 0.3 | 3.1 | 1.5 | 3.4 | 0.2 | 6.5 | 1.7 |
| **Geranium viscosissimum** | 27.5 | 25.0 | 2.3 | 2.3 | 2.9 | 3.8 | 2.4 | 1.7 | 5.2 | 5.4 |
| **Bromus mollis** | 27.5 | | 1.4 | | 2.9 | | 1.5 | | 3.3 | |
| **Heuchera cylindrica** | 25.0 | 20.0 | 4.0 | 1.8 | 2.6 | 3.0 | 4.1 | 1.3 | 6.7 | 4.3 |
| **Agropyron spicatum** | 25.0 | | 2.3 | | 2.6 | | 2.3 | | 4.9 | |
| **Rosa nutkana** | 5.0 | 22.5 | 0.5 | 2.8 | 0.5 | 3.4 | 0.5 | 2.1 | 1.0 | 5.5 |
| **Lupinus laxiflorus** | 22.5 | | 2.5 | | 2.3 | | 2.5 | | 4.8 | |
| **Helianthella uniflora** | 22.5 | | 2.5 | | 2.3 | | 2.5 | | 4.8 | |
| **Iris missouriensis** | | 22.5 | | 1.0 | | 3.4 | | 0.7 | | 4.1 |
| **Epilobium paniculatum** | 20.0 | | 1.2 | | 2.1 | | 1.2 | | 3.3 | |
| **Gaillardia aristata** | 17.5 | | 0.8 | | 1.8 | | 0.8 | | 2.7 | |
| **Amelanchier alnifolia** | | 15.0 | | 2.8 | | 2.3 | | 2.1 | | 4.4 |
| **Sisyrinchium inflatum** | 15.0 | | 0.8 | | 1.6 | | 0.8 | | 2.3 | |
| **Lithophragma** sp. | 15.0 | | 0.8 | | 1.6 | | 0.8 | | 2.3 | |
| **Castilleja lutescens** | 12.5 | | 0.6 | | 1.3 | | 0.6 | | 1.9 | |
| **Hieracium albertinum** | 12.5 | 2.5 | 2.2 | 0.1 | 1.3 | 0.4 | 2.2 | 0.1 | 3.5 | 0.4 |
| **Wyethia amplexicaulis** | | 10.0 | | 3.5 | | 1.5 | | 2.6 | | 4.1 |
| **Lupinus sericeus** | 5.0 | 10.0 | 0.2 | 0.6 | 0.5 | 1.5 | 0.2 | 0.4 | 0.7 | 1.9 |
| **Hypericum perforatum** | | 10.0 | | 0.6 | | 1.5 | | 0.2 | | 1.7 |
| **Erythronium grandiflorum** | 10.0 | | 0.6 | | 1.0 | | 0.2 | | 1.7 | |
| **Microsteris humilis** | 10.0 | | 0.3 | | 1.0 | | 0.3 | | 1.4 | |
| **Cirsium sp.** | 10.0 | | 0.9 | | 1.0 | | 0.9 | | 2.0 | |

TABLE 7. (Continued)

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Besseya rubra** | 7.5 | | 0.2 | | 0.8 | | 0.2 | | 1.0 | |
| **Lactuca serriola** | 5.0 | | 0.2 | | 0.5 | | 0.2 | | 0.7 | |
| **Calochortus elegans** | 5.0 | | 0.2 | | 0.5 | | 0.2 | | 0.7 | |
| **Draba verna** | 5.0 | | 0.2 | | 0.5 | | 0.2 | | 0.7 | |
| **Solidago missouriensis** | 5.0 | | 0.5 | | 0.5 | | 0.7 | | 1.0 | |
| **Spireaea betulifolia** | 5.0 | 2.5 | 0.5 | 0.4 | 0.5 | 0.4 | 0.7 | 0.3 | 1.0 | 0.7 |
| **Poa pratensis** | | 2.5 | | 0.1 | | 0.4 | | 0.1 | | 0.4 |
| **Potentilla arguta** | | 2.5 | | 0.4 | | 0.4 | | 0.3 | | 0.7 |
| **Antennaria luzuloides** | 2.5 | | 0.4 | | 0.3 | | 0.4 | | 0.7 | |
| **Festuca pacifica** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Koeleria cristata** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Perideridia gairdneri** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Anemone piperi** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Brodiaea douglasii** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Myosotis stricta** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Claytonia perfoliata** var. **depressa** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Holosteum umbellatum** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Bromus tectorum** | 2.5 | | 0.1 | | 0.3 | | 0.1 | | 0.3 | |
| **Lithospermum ruderale** | 2.5 | | 2.2 | | 0.3 | | 2.2 | | 0.5 | |

TABLE 8. A comparison of frequencies, coverages, and importance values of the dominant species and of some of the more important subordinant species in the tall shrub and rose communities at Site II. Frequencies and coverages were converted to relative frequencies and relative coverages to obtain important values.

| Species | Frequency | | Coverage | | Importance Value | |
|---|---|---|---|---|---|---|
| | Tall Sh. Com. | Rose Com. | Tall Sh. Com. | Rose Com. | Tall Sh. Com. | Rose Com. |
| **Crataegus douglasii** | 70.0 | 10.0 | 46.9 | 0.3 | 31.0 | 0.8 |
| **Prunus virginiana** | 50.0 | 10.0 | 10.1 | 0.9 | 9.2 | 1.2 |
| **Amelanchier alnifolia** | 40.0 | 30.0 | 3.8 | 4.0 | 5.0 | 4.4 |
| **Rosa nutkana** | 100.0 | 90.0 | 13.0 | 20.5 | 14.3 | 19.0 |
| **Symphoricarpos albus** | 100.0 | 100.0 | 30.1 | 4.3 | 23.8 | 8.9 |
| **Spiraea betulifolia** var. **lucida** | 40.0 | 40.0 | 2.4 | 1.2 | 4.2 | 3.2 |
| **Geranium viscosissimum** | 80.0 | 80.0 | 2.4 | 12.9 | 7.0 | 13.4 |
| **Potentilla gracilis** var. **flabelliformis** | 50.0 | 95.0 | 1.5 | 10.7 | 4.4 | 12.8 |
| **Carex geyeri** | 70.0 | 90.0 | 15.2 | 3.4 | 13.4 | 7.7 |
| **Galium aparine** | 90.0 | 5.0 | 8.8 | 0.2 | 11.3 | 0.4 |
| **Epilobium angustifolium** | 100.0 | 35.0 | 4.3 | 3.7 | 9.5 | 4.5 |
| Sum of I.V.s for the three tall shrubs (**A. alnifolia, C. douglasii,** and **P. virginia**) | | | | | 45.2 | 6.4 |
| Sum of I.V.s for the three low shrubs **R. nutkana, S. betulifolia,** and **S. albus**) | | | | | 42.3 | 31.1 |

II and Tall shrub II (36.9), and between Grass II and Rose II (46.5) (note comparisons 8 and 5, Table 5). Although *Rosa nutkana* is present in the grass community at Site II, it has an I.V. of only 1.0 compared with its I.V. of 19.0 in the Rose II community (Table 8).

At Site III, two stands dominated by Idaho fescue were noted but not sampled. Their resemblance to Grass II was so striking as to make them at once recognizable.

A sampling of the soil in one of these stands at Site III showed an almost identical profile to that in Grass II—namely, a restrictive clay layer at 45 to 55 cm. Therefore, we propose that Grass II and the two grass stands at Site III are discrete communities and together should be considered as a possible heretofore unrecognized *Festuca* phase of Daubenmire's *Festuca-Symphoricarpos* Association restricted to north slopes with a unique soil profile.

*Rose and Tall-shrub Communities.* These two communities with an I.S. of 59.1 obviously resemble each other closely. Tall shrub species are few in number and have a very low combined I.V. (6.4) in the rose community; at the same time, the low shrub species are well represented in the tall shrub community with a combined I.V. of 42.3 (Table 8). A difference is to be noted in the I.V.s of *Geranium viscosissimum* and *Potentilla gracilis* var. *flabelliformis*, both relatively shade intolerant species with higher quantitative values in the rose community. By contrast, *Galium aparine* has an I.V. of 28 times greater in the tall shrub community than in the rose community. This finding perhaps reflects a response to a slight difference in microclimate such as deeper shade and protection from desiccating winds. The rose community is composed of four synusiae (the low shrub layer, a tall forb layer, a low forb layer, and a ground cover of cryptogams); the tall shrub community is comprised of these four layers plus a fifth, the tall shrub synusia itself. Distinctive differences occur between the soil profile of

the tall shrub and the other communities (Fig. 1). In addition, there are distinctive differences noted for the rose community.

On the basis of the available data, the tall shrub community clearly belongs to Daubenmire's *Crataegus-Symphoricarpos* Association (1970) as an edaphic community. On the steep north slopes we analyzed, the community is discrete and its boundaries are limited by a particular soil profile.

The rose stands are quite distinct and readily recognizable at all three sites. We found no evidence to suggest that they are seral communities. The presence of a *Symphoricarpos* union in this community precludes classifying it as Daubenmire's *Festuca idahoensis-Rosa nutkana* Association (1970). So, too, this habitat type is reputedly restricted to the rainshadow of the Blue Mountains (Daubenmire, 1970). In our study area, the rose stems range in height from 0.7 m to 1.0 m. They regularly flower and set fruit. Daubenmire (1970) describes a *Symphoricarpos* phase of his *Festuca idahoensis-Symphoricarpos albus* Association in which *Rosa nutkana* and *R. woodsii* comprise a central core surrounded by *Symphoricarpos* (snowberry). No such zonation is noted in the stands of this study. Rose and snowberry are intermingled, with the rose overtopping the snowberry and consistently exceeding it in both frequency and coverage. For example, at Site II *Rosa nutkana* had an I.V. of 19.0 compared to the I.V. of *Symphoricarpos albus* of 8.9. These rose dominated thickets are apparently included by Daubenmire (1970) under his *Symphoricarpos* phase of the *Festuca idahoensis-Symphoricarpos albus* Association. However, on the basis of our limited sampling of these communities, a *Rosa* phase would seem to be at least an equally appropriate designation, if not, indeed, more appropriate.

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# Improved Efficiency in Weight Scaling Operations through Post-Stratification Techniques

**Abstract**

Weight scaling procedures are used in many parts of the world for stumpage assessments and for payroll and production control. The study described herein considers the improvement in the estimate of the total volume of wood using post-stratification techniques and the weight scaling procedure. The authors recommend that post-stratification by arrival of truck loads should be used in determining an estimate and the precision of the total volume of wood taken out of the forest.

## Introduction

The scaling of logs by weight (simply, weight scaling) is a technique for estimating the volume of wood taken out of the forest. The technique relies on the theory of ratio estimation of sample volume of truck loads (variable of interest) to sample load weight (auxiliary variable). The ratio is then multiplied by the total weight of all loads to give an estimate of the total volume of logs taken out of the forest during a particular year or period of operation. The application is an extremely practical and important one since weight scaling is practiced in many parts of the world at the present time, and is the basis not only for stumpage assessment (British Columbia Forest Service, 1975), but for payroll and production control. A reviewer of this paper indicated that the justification for weight scaling in the Pacific Northwest is for accountability so that drivers can receive payment!

The procedure begins with the determination of the number of samples required for achieving a certain desired precision. The sample is then obtained using any appropriate sampling procedure, and taking from that sample the volumes (scales) and the respective weights. All other log loads not scaled are weighed to give complete knowledge of the auxiliary population.

Since sample loads are heterogeneous in nature, the sampling procedure must ensure adequate representation of the various strata or classes. Otherwise, imprecise estimate is likely to be obtained. Cochran (1963) has suggested the use of stratification-after-sampling (post-stratification) techniques for such samples. Wensel (1974) demonstrated (with Chamber Creek #13 scale data) that a considerable gain in precision could be expected if post-stratification is done on the basis of two scale volumes. The procedure discussed in this paper considers post-stratification procedures on the sample scale data collected, and are based on "arrivals of truck loads" and "the

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weight classes" of the loads. It is likely, but not necessarily true, that the latter stratification procedure may correspond with different species groups.

### Weight Scaling Procedure

We consider a population of N loads from which a random sample of size n is to be collected. All trucks arriving at the check-point are weighed. Those trucks falling in the sample are offloaded, and the volume and weight of their loads are taken. The order in which the samples are weighed is noted.

If use is not made of the ratio of volume to weight (r) the standard error of the mean volume estimate

$$\bar{y}_1 = (\Sigma y_i)/n \qquad (1)$$

is given as

$$\text{SYBAR} = \left\{ \frac{N-n}{Nn(n-1)} \sum^{n} (y_i - \bar{y}_1)^2 \right\}^{1/2} \qquad (2)$$

where $y_i$ represents the volume from the ith sample.

If use is made of the ratio estimate, as is usually the case with weight scaling, an improved estimate of the mean volume is given by

$$\bar{y}_2 = \frac{\frac{\Sigma y_i}{n}}{\frac{\Sigma x_i}{N}}$$

$$= r\,\mu_x \qquad (3)$$

with a standard error SYBAR.R, given by equation (4)

$$\text{SYBAR.R} = \left\{ \frac{N-n}{Nn} (\Sigma y_i^2 - 2r\Sigma x_i y_i + r^2 \Sigma x_i^2) \right\}^{1/2}$$

$$= \left\{ \frac{N-n}{Nn} (s^2 - 2rs_{xy} + r^2 s_x^2) \right\}^{1/2} \qquad (4)$$

where $x_i$ represents the ith sample weight (auxiliary variate), and $s_x^2$, $s_x^2$, $s_{xy}$ represent the variances of y, x and the covariance of x and y.

### Post-Stratification Applied to Weight Scaling Data by Weight Classes

The sample data obtained from the above scaling procedure may now be divided into various weight classes (5, 10, 15, 20, etc.) as given in Tables 1 and 2. This procedure may simply be referred to as post-stratification by weight since the stratification is done after sampling. It must be emphasized that the data represent sample loads (n), and as such $N_h$'s (that is, class or stratum sizes) may be assumed to be known.[2] Stratum weight ($N_h$ /N) may not be reasonably estimated by $\frac{n_h}{n}$, where $n_h$ represents the number of units in the sample that belong to the $h^{th}$ class or stratum.

[2] $N_h$'s would have been known if stratification had been made before the sampling or approximately known if the method of quota sampling had been used to obtain n.

TABLE 1. Log scaling data summary for Company M, Prince George District—10 post-weight classes, data converted from imperial units. (Source: Nokoe, 1976.)

| X-cell limits (kg) | Frequency (no. of loads) | X variance ($kg^2 x 10^6$) | Y variance $(cub.\ meter)^2$ | Ratio ($m^3/kg$) |
|---|---|---|---|---|
| 9752-16781 | 16 | 1.44 | 1.98 | .00121 |
| 16781-23810 | 1 | 0.00 | 0.00 | .00144 |
| 23810-30839 | 47 | 1.06 | 6.90 | .00126 |
| 30839-37868 | 76 | 3.55 | 9.15 | .00126 |
| 37868-44897 | 13 | 5.74 | 8.70 | .00127 |
| 44897-51926 | 19 | 4.82 | 20.67 | .00126 |
| 51926-58955 | 12 | 4.07 | 15.89 | .00125 |
| 58955-65984 | 24 | 3.33 | 9.02 | .00125 |
| 65984-73013 | 16 | 4.24 | 17.63 | .00124 |
| 73013-80042 | 14 | 3.77 | 28.35 | .00125 |

TABLE 2. Log scaling data summary for Company E, Nelson District—5 post-weight classes.

| X-cell limits (kg) | Frequency (no. of loads) | X variance ($kg^2 x 10^6$) | Y variance $(cub.\ meter)^2$ | Ratio ($m^3/kg$) |
|---|---|---|---|---|
| 475- 903 | 2 | 2.99 | 7.42 | .00114 |
| 903-1331 | 28 | 3.82 | 17.10 | .00147 |
| 1331-1759 | 139 | 3.37 | 17.37 | .00125 |
| 1759-2187 | 152 | 3.01 | 15.83 | .00121 |
| 2187-2615 | 7 | 6.39 | 11.03 | .00120 |

The weight estimate of the mean volume may be given by

$$y_3 = \frac{\Sigma^{N}h\ y_h}{N} \qquad (5)$$

with an error given by

$$P.SYBAR.R^3 = \left\{ \frac{N-n}{Nn} \sum^{st} \frac{^{N}h\ s_h^2}{N} + \frac{1}{N^2} \sum^{st} \frac{^{N-N}h\ s_h^2}{N} \right\}^{1/2} \qquad (6)$$

where: $\frac{N_h}{N}$ is estimated by $\frac{n_h}{n}$, and N is assumed to be reasonably large so that $\frac{n}{N}$ is negligible. $\frac{^{N-N}h}{N}$ reduces to $\frac{^{n-n}h}{n}$. Also, $s_h^2$ represent the stratum variance using equation (4) and st represents the number of classes or strata.

### Post-Stratification by Arrivals of Truck Loads

The post-stratification by arrivals of truck loads simply requires equal sub-division of the scale data as recorded on the weight-scaling data sheet into as many classes as desired. This procedure is simpler and faster than that of determining weight classes. The same computational formulae for weight classes may be used. It may, however, be noted that whereas post-stratification by arrivals uses equal allocation of sample to strata procedures, that of weight classes makes use of proportional allocation.

[3]The 2nd term in equation (6) is the extra term brought about as a result of $n_h$ not distributing itself in the same manner as $N_h$ (Cochran, 1963). Further notes: SYBAR = standard error without using ratio estimation; SYBAR.R = standard error using ratio estimation; and P.SYBAR.R = standard error for estimate based on both ratio estimation and stratification procedures.

The four computational procedures, representing the four different uses of the scale data, were applied to thirteen sets of sample load data made available by companies operating in British Columbia (Nokoe, 1976). Due to limitations of space, results for only five data sets from Vancouver, Nelson, Prince George, Cariboo, and Kamloops districts of British Columbia are given here. The original data for this study were in imperial units, but the results given here are in metric units. A hypothetical example in the absence of the original data on the computational procedures is given in the Appendix. The summary at the end of the Appendix shows the general advantage (note the coefficients of variation) of the post-stratification procedures over the non-stratification method.

#### Results and Discussion

Computed standard errors for the five sample scale data are given in Table 3. Weight and volume are known to be highly correlated, which is a necessary requirement for using ratio estimation procedures. Therefore, the general improvement in efficiency of weight scaling (ratio estimation) procedures over non-ratio (SYBAR) was not unexpected. The efficiency was more enhanced for the Prince George and Vancouver (coast) districts data, probably because of the wide variability in coastal data.

Estimates based on weight or arrival of truck loads were generally more efficient than the non-stratification procedures. Stratification ensured homogeneous groups, and as such, combined standard error estimates were expected in theory to be smaller than those obtained from a single set of sample from the heterogeneous population.

It was also evident that for the two stratification criteria, an increase in the number of sub-divisions implied an increase in efficiency. Possibly the extension resulted in more homogeneous sub-groups. An optimum number of sub-divisions was not

TABLE 3. Standard errors of estimates of mean volume of logs in cubic meters.

| Company | Data Source (British Columbia) | Number of Sub-divisions | No stratification | | Post-stratification | |
|---|---|---|---|---|---|---|
| | | | No ratio SYBAR | With ratio SYBAR.R | With ratio By weight | With ratio By arrival |
| A | Kamloops | 5 | 5.32 | 3.33 | 1.92 | 0.99 |
| | | 10 | 5.32 | 3.33 | 1.44 | 0.73 |
| | | 15 | 5.32 | 3.33 | 1.17 | 0.58 |
| | | 20 | 5.32 | 3.33 | 1.03 | 0.46 |
| D | Cariboo | 5 | 3.74 | 2.36 | 1.19 | 0.84 |
| | | 10 | 3.74 | 2.36 | 0.86 | 0.63 |
| | | 15 | 3.74 | 2.36 | 0.73 | 0.50 |
| | | 20 | 3.74 | 2.36 | 0.65 | 0.43 |
| M | Prince George | 5 | 21.68 | 2.66 | 1.35 | 1.03 |
| | | 10 | 21.68 | 2.66 | 0.98 | 0.77 |
| | | 15 | 21.68 | 2.66 | 0.89 | 0.62 |
| | | 20 | 21.68 | 2.66 | 0.78 | 0.55 |
| E | Nelson | 5 | 5.69 | 3.79 | 2.27 | 1.43 |
| | | 10 | 5.69 | 3.79 | 1.73 | 0.98 |
| | | 15 | 5.69 | 3.79 | 1.47 | 0.68 |
| | | 20 | 5.69 | 3.79 | 1.28 | 0.61 |
| H | Vancounver | 5 | 8.40 | 4.26 | 2.65 | 1.35 |
| | | 10 | 8.40 | 4.26 | 1.97 | 0.97 |
| | | 15 | 8.40 | 4.26 | 1.60 | 0.78 |
| | | 20 | 8.40 | 4.26 | 1.42 | 0.65 |
| Hypothetical example (Appendix I) | | 2 | 0.37 | 0.38 | 0.11 | 0.10 |

determined in this study, but we feel this area should form the basis of future research.

Based on the scale data available for the study and the results obtained, we recommend that post-stratification based on arrival of truck loads be incorporated in weight scaling procedures. The method involves routine manipulation of the data as recorded on the designed weight-scaling data sheet, and does not interfere with current weight scaling practices.

## APPENDIX

### Illustration of Computational Procedures with Hypothetical Scale Data

| Order of arrivals | i | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Weight, | $X^i$ | 4 | 2 | 10 | 5 | 8 | 3 | 14 | 2 | 5 | 3 |
| Volume, | $y^i$ | .8 | .25 | 2 | 1.2 | 2.3 | 10 | 4.2 | 0.3 | 0.8 | 1.2 |

Assume $N = 1000$ and $\Sigma_N x_i = 6000$. Thus $\mu_x = 6.0$

### Estimates and Standard Errors

(i) No stratification, no use of ratio:

$\bar{y}_1 = (.8 + \ldots + 1.2)/10 = 1.405$ (1)

$$SYBAR^2 = \frac{1000 - 10}{(1000)(10)(9)} \left\{(.8 - 1.405)^2 + \ldots + (1.2 - 1.405)^2\right\} = .1375$$

$\therefore$ SYBAR $= \underline{0.3708}$ (2)

(ii) No stratification, use of ratio:

$\Sigma y_i = 14.05 \qquad \Sigma x_i = 56$

$\Sigma y_i = .8^2 + \ldots + 1.2^2 = 32.2425$

$\Sigma x_i = 4^2 + \ldots + 3^2 = 452$

$\Sigma x_i y_i = (4)(.8) + \ldots + (3)(1.2) = 118.1$

$r = (14.05)/56 = 0.25089$

$\therefore\ y_2 = r\,\mu_x = 1.506$ (3)

$$SYBAR.R^2 = \frac{1000 - 10}{(1000)(10)} \left(\Sigma y^2 - 2r\,\Sigma xy + r^2\,\Sigma x^2 = 0.1420\right)$$

$SYBAR.R = \underline{0.3768}$ (4)

(iii) Post-stratification, use of ratio:

### By Order of Arrivals

If we consider only two classes, the sample of size 10 is split into 2, i.e., $i = 1, \ldots, 5$ and $i = 6, \ldots, 10$.

Computational formulae from (ii) are applied to each class.

For Class 1 $i = 1, 2, 3, 4, 5$:

$\Sigma y_i = 6.55 \qquad \Sigma y_i^2 = 11.4325 \qquad \Sigma x_i y_i = 48.1$

$\Sigma x_i = 29 \qquad \Sigma x_i^2 = 209$

$\therefore\ \bar{y}_2 = r\,\mu_x = 1.355$ and $r = 0.2259$

$$\text{with } s_1^2 = \frac{1000 - 5}{(1000)(5)} \left\{\Sigma y^2 - 2r\,\Sigma xy + r^2\,\Sigma x^2\right\} = 0.0729$$

For class 2 $i = 6, 7, 8, 9, 10$:

$\Sigma y_i = 7.50 \qquad \Sigma y_i^2 = 20.81 \qquad \Sigma x_i y_i = 70$

$\Sigma x_i = 27 \qquad \Sigma x_i^2 = 243 \qquad r = 0.2778$

$\therefore\ y_2 = r\,\mu_x = 1.667$

$$\text{with } s_2^2 \frac{1000 - 5}{(1000)(5)} \left\{\Sigma y^2 - 2r\,\Sigma yx + r^2\,\Sigma x^2\right\} = 0.1341$$

Thus weighted estimates from classes 1 and 2 are:

$y_3 = \frac{5(1.355) + 5(1.667)}{10} = 1.511$ (5)

and

$$P.SYBAR.R^2 = \frac{1000-10}{(1000)(10)}\left\{\frac{5}{10}(s_1^2 \cdot s_2^2) + \frac{1}{100}\left(\frac{10-5}{10}\right)(s_1^2 + s_2^2)\right\} = .01044$$

$$\therefore P.SYBAR.R = \underline{0.1022}$$

## By Weight Classes

We consider only 2 weight classes of equal width:
$x_i = 2$ to 8 and $x_i = 8$ to 14

| x − class | Freq | $\Sigma x_i$ | $\Sigma y_i$ | r | $\Sigma y_i^2$ | $\Sigma x_i^2$ | $\Sigma xy$ | $\overline{y}_2$ | $s_h^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 2 − 8 | 7 | 24 | 5.55 | .2313 | 5.3125 | 92 | 209 | 1.3878 | .0803 |
| 8 − 10 | 3+ | 22 | 8.5 | .2656 | 26.93 | 360 | 97.2 | 1.5936 | .2303 |

(+ The corresponding units are i = 3, 5, 14)
The r's and S's are obtained using the same method as order of arrivals

$$\overline{y}_3 = \frac{7(1.3878) + 3(1.5936)}{10} = 1.450 \qquad (5)$$

and

$$P.SYBAR.R^2 = \frac{1000-10}{(1000)(10)}\left[\frac{7s^2 + 3s^2}{10} + \frac{1}{100}(3s_1 + 7s_2)\right] = .0127$$

$$\therefore PSYBAR.R = \underline{0.1127} \qquad (6)$$

## SUMMARY

| | No stratification | | Stratification with ratio | |
|---|---|---|---|---|
| | No ratio | With ratio | By weight | By arrival |
| $\bar{y}$ | 1.405 | 1.506 | 1.450 | 1.511 |
| $S_{\bar{y}}$ | 0.3708 | 0.3768 | 0.1127 | 0.1022 |
| CV | 26% | 25% | 8% | 7% |

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# $^{210}$Pb Geochronology and Trace Metal Concentrations of Sediments from Upper Klamath Lake and Lake Euwana, Oregon

**Abstract**

Rates of sedimentation calculated from analyses of $^{210}$Pb activities in cores from two shallow lakes whose mean depths are 2.4 m, Upper Klamath Lake and Lake Euwana (Klamath County, Oregon), indicate that they are filling at approximately 3.0 mm/yr. Average sedimentation rates for compaction-corrected cores range from 0.9 mm/yr to 8.5 mm/yr or from 0.03 g/cm$^2$/yr to 0.48 g/cm$^2$/yr, respectively. Plots of excess $^{210}$Pb activity versus depth show a mixing layer due to biological activity and other physical mixing that ranges in thickness from 5 to 20 cm, and that is found below the sediment-water interface at all coring locations. Trace metal analyses performed to establish baseline levels of selected elements show very low concentrations of all metals measured in cores from Upper Klamath Lake (Cd, Cu, Cr, Fe, Pb, Mn, and Zn) when compared with concentrations of these metals found in other North American lacustrine environments.

## Introduction

The first reported use of $^{210}$Pb dating was in the early 1960s to determine snow accumulations in the permanent snowfields of Greenland (Goldberg, 1963). This radiometric method has since been used as a sedimentological tool to examine accumulation rates in a variety of sedimentary environments, which range from the relatively calm environments of rivers, estuaries, and lakes (Benninger, 1976; Benninger *et al.*, 1975, 1976; Martin, 1979; Koide *et al.*, 1973; Edgington and Robbins, 1976; Matsumoto, 1975; Bruland *et al.*, 1974, and Thomson *et al.*, 1975) to the more dynamic environments of continental shelves and slopes (Nittrouer *et al.*, 1979; Shokes and Presley, 1976; Bothner and Locker, 1977; Holmes and Martin, 1977, 1978; Koide *et al.*, 1972).

This study was undertaken in response to concern expressed by citizens that Upper Klamath Lake was undergoing significant sediment deposition. This possible accumulation of sediment could decrease the use of the lake as a water-supply reservoir and could damage the wildlife habitat and recreation potential. Traditional methods of determining sedimentation rates based on stratigraphic methods or C-14 dating often provide only averages of historical rates for thousands of years over several meters of sediment; generally, they do not adequately reflect recent, shorter term accumulation. $^{210}$Pb-determined rates are more reflective of modern sedimentation that has occurred during the past 100-150 years. Sedimentation rates calculated from $^{210}$Pb activities in many lakes have been found to be in agreement with rates derived from more time consuming established palynological methods (Robbins and Edgington, 1975). $^{210}$Pb appeared to be a tool well suited to examine the recent sedimentation and to estimate the future accumulation rates of Upper Klamath Lake and Lake Euwana.

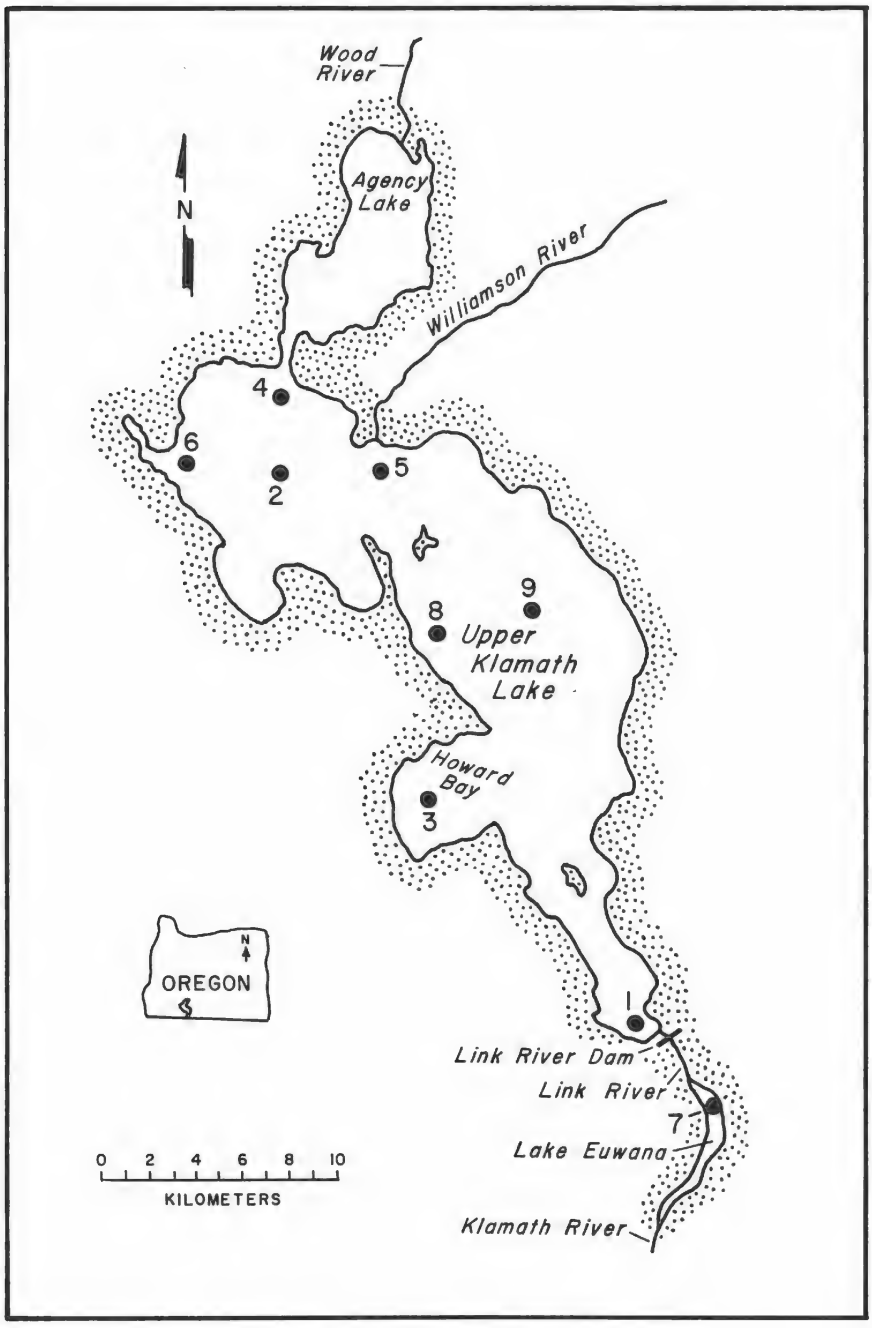


Figure 1. Sample locations, Upper Klamath Lake and Lake Euwana, Oregon.

### Geologic Setting

Upper Klamath Lake is located east of the Cascade Mountains in southwestern Oregon between Crater Lake National Park and the city of Klamath Falls. It is a large, shallow lake that has a surface area of 310 $km^2$ and a mean depth of 2.4 m. Lake Euwana is located approximately 3 km downstream from the outlet of Upper Klamath Lake (Fig. 1). The water level of Upper Klamath Lake is controlled between 1261 and 1264 m above sea level by a dam constructed in 1917 by the Bureau of Reclamation at the outlet of the lake into the Link River. This controlled level allows the lake to be used as a reservoir for hydroelectric power production and for irrigation water. Much of the watershed of Upper Klamath Lake (9850 $km^2$) is located in mountainous areas which are abundant in volcanic pumice derived during the formation of the Crater Lake Caldera about 45 km to the northwest (Gahler and Sanville, 1971). The watershed contains many natural marshes and reclaimed agricultural land. Water is supplied to Upper Klamath Lake by the Williamson River, a major tributary that accounts for approximately 46 percent of the lake input. The Wood River, via Agency Lake, accounts for about 15 percent of the input; the remainder is derived from springs, irrigation canals, and agricultural drainage (Miller and Tash, 1967). The dam accounts for 78 percent of the total outflow, with remaining amounts leaving by evaporation and withdrawal by irrigation pumping. Discharge from Upper Klamath Lake via the dam flows into the Link River, passes through shallow Lake Euwana into the Klamath River, and eventually flows through northern California on its way to the Pacific Ocean 386 km away.

## Sample Collection and Handling

### Field Collection

Core samples of lakebed material were taken at eight sites in Upper Klamath Lake and one site in Lake Euwana. Sampling sites were chosen to represent a variety of bottom-sediment types, water depths, shoreline configurations, and lake currents (Fig. 1, Table 1). Cores 7 cm in diameter and averaging 50 cm in length were obtained by two divers using a coring system designed to retrieve cores from soft sediments such as those found in Upper Klamath Lake and Lake Euwana with only minimal

TABLE 1. Characteristics of cores and rates of sediment accumulation.

| Core number | Location* | Water depth (m) | Core length (cm) | Rate of sedimentation (mm/yr) | Rate of accumulation x $10^{-2}$ ($g/cm^2/yr$) |
|---|---|---|---|---|---|
| 1 | UKL; near lake outlet | 1.9 | 40 | 1.8 | 8.6 |
| 2 | UKL; central portion of lake | 2.0 | 46 | 4.5 | 13.5 |
| 3 | Howard Bay | 0.8 | 65 | 0.9 | 2.7 |
| 4 | UKL; Agency Lake outlet | 0.8 | 62 | 8.5 | 48.2 |
| 5 | UKL; Williamson River outlet | 1.0 | 45 | 1.6 | 21.0 |
| 6 | UKL; suspected low velocity currents | 1.0 | 60 | 1.9/0.4 | 6.9/1.5 |
| 7 | Lake Euwana | 2.2 | 48 | 2.9 | 11.9 |
| 8 | UKL; suspected high velocity currents | 6.1 | 39 | 3.2 | 12.4 |
| 9 | UKL; central portion of lake | 2.3 | 47 | 1.2 | 3.7 |

*Core locations shown in Fig. 1; UKL = Upper Klamath Lake.

disturbance to the sediment-water interface. A split hydroplastic core barrel, which had been taped together, was slowly pushed into the sediment. Once the corer had been inserted, an aluminum handle was attached, the open barrel was plugged with a PVC (polyvinyl chloride) cap, and the system was pulled from the sediment. A cap was placed over the lower end of the core before it was transported to the surface. The core was split in the field using a stainless steel wire. Half of the core was stored for X-radiography and trace-metal analyses; the remaining half was sampled for $^{210}Pb$ analyses.

### Laboratory Methods

X-radiographs were made of the unsampled core halves to examine the amount of reworking by benthic organisms, the presence of burrows, structural elements and discontinuities, and any evidence of disturbances incurred during the coring operation. X-radiographs also were examined to confirm field observations, and to reveal features not readily apparent by visual examination of the cores.

Sediment samples for radiometric determinations were analyzed using a modification of the method described by Flynn (1968). Secular equilibrium was assumed between $^{210}Pb$ and $^{210}Po$. The details of the procedure are presented in Martin and Rice (1980). Generally, sediment subsamples were weighed, dried at 100°C, and reweighed to determine the moisture content. The dried sample then was ground and dry ashed to remove organic matter. Ashed samples were spiked with a known amount of calibrated $^{208}Po$ and subjected to a series of $HNO_3$, HCl, and $H_2O_2$ additions. The final solution was pH adjusted and the polonium was autoplated onto a silver planchet. The planchets were alpha counted on a multichannel analyzer equipped with silicon surface barrier detectors. To provide a 3-4 percent confidence level in the activity values, a minimum of 750-1000 counts were obtained for each planchet.

For trace metal determinations, 1 g subsamples were weighed, heated in a muffle furnace at 450°C for 6 hrs, cooled in a desiccator, and reweighed. Ashed samples were transferred to precleaned culture tubes, digested in concentrated reagent-grade nitric acid, and analyzed by standard atomic absorption methods.

## $^{210}Pb$ Theory and Assumptions

The method used in this study for determining sedimentation rates is based on the occurrence of excess radioactive lead, $^{210}Pb$, which is a naturally occurring member of the uranium 238 decay series. Radon-222, which has a half life of 3.8 days (Lederer *et al.*, 1968), diffuses from the soil into the atmosphere and remains chemically inert until it decays through four short-lived nuclides ($^{218}Po$, $^{214}Pb$, $^{214}Bi$, and $^{214}Po$) to $^{210}Pb$. This isotope is rapidly removed from the atmosphere into the hydrosphere by rain, snow, and dry fallout; it provides a measurable flux to the land and waters of approximately 0.9 to 1.0 dpm $^{210}Pb/cm^2/yr$ (Benninger, 1976). $^{210}Pb$ is also supplied to the hydrosphere by stream runoff and decay of $^{226}Ra$ in the water column; however, these sources are not significant when compared with the atmospheric source (Benninger, 1976). There seems to be no significant formation of $^{210}Pb$ in nuclear detonations (Beasley, 1969). It is rapidly removed from the water column and accumulated in the bottom sediments. Several mechanisms have been proposed for the removal of

$^{210}$Pb from the hydrosphere including adsorption onto biogenic and/or nonbiogenic material and coprecipitation with Fe and Mn oxides. The chemical behavior of lead makes it immobile in the sediments. Once in the sediment column, $^{210}$Pb, which has a half life of 22.26 years (Höhndorf, 1969), undergoes a beta decay to $^{210}$Bi. This daughter undergoes another decay to $^{210}$Po, which has a half life of 138.4 days (Lederer *et al.*, 1968) and alpha decays to stable $^{206}$Pb. If secular equilibrium is assumed to exist between $^{210}$Pb and $^{210}$Po, which has been investigated (Benninger, 1976; Nittrouer *et al.*, 1979) and found to be a reasonable assumption, the alpha decay of $^{210}$Po can be used to measure the $^{210}$Pb activity of both the $^{210}$Pb produced by the decay of $^{226}$Ra in the sediment column (supported $^{210}$Pb) and $^{210}$Pb added from external sources (excess $^{210}$Pb). This technique has been used by many investigators (Robbins and Edgington, 1975; Flynn, 1968; Millard, 1963; Nozaki and Tsunogai, 1973). A calibrated $^{208}$Po spike is used to calculate the activity of the $^{210}$Po and standard methods of data reduction are used to obtain $^{210}$Pb activities. The supported $^{210}$Pb activity found to be in equilibrium with its parent $^{226}$Ra is indirectly determined by assuming that radioactive equilibrium is attained in the lower sections of the core which show constant $^{210}$Pb activity with depth. This supported activity is subtracted from the total activity in the upper portions of the core to obtain excess $^{210}$Pb activities. Excess $^{210}$Pb activity decreases at a rate controlled by its half life. Sediment rates are calculated by plotting the log (1n) of the excess $^{210}$Pb activities versus depth and calculating time horizons over intervals of constant slope using the equation:

$$A_d = A_o e^{-\lambda t}$$

Where $A_d$ = activity of $^{210}$Pb at a depth d
$A_o$ = activity of $^{210}$Pb at a higher reference point
$\lambda$ = decay constant of $^{210}$Pb
$t$ = age of the sediment sample

#### Results and Implications

##### Texture

A general relationship between texture and $^{210}$Pb activity indicates that higher activities are associated with finer sediments (Nittrouer *et al.*, 1979). Textural measurements provide information to identify significant grain-size fluctuations within each core which can affect interpretation of the $^{210}$Pb geochronology. Textural parameters were not measured in the cores taken for this study; however, field observations indicate that, other than a few pumice layers, the sediment texture within each core appeared to be silty clay and relatively homogeneous. Other investigators have found that the sediments of Upper Klamath Lake are silty clay, neutral to slightly acidic, noncalcareous, quite uniform in texture, and composed of diatoms, organic matter, and clay minerals. These other investigators found major clay-mineral components to be chlorite, vermiculite, and mica (Gahler and Sanville, 1971). There are pumice layers in cores 1 and 7 about 40 cm down the core. Core 5 contains a large amount of pumice in the top 17 cm which may have been carried by the Williamson River into Upper Klamath Lake during a period of high-energy flow from the watershed.

##### Moisture Content

The moisture content of the cores is very high and uniform, ranging from 85-92 per-

cent just below the sediment-water interface to 81-88 percent approximately 60 cm below the surface. Detailed moisture data for these cores are presented elsewhere (Martin and Rice, 1980). These values are in very good agreement with values obtained by other investigators who found 88-92 percent moisture content at the water interface and from 80-88 percent 120 cm below the surface (Gahler and Sanville, 1971). The water content varied in several intervals of core 5 because of the presence of layers of pumice or pumice-like material; the water content of the rest of the core was uniform. Moisture content of each core was used to correct the length of the core for compaction, which is explained in the sedimentation section of this paper.

### Bioturbation and Mixing

Physical and chemical processes that disturb the sediments after they have been deposited are very important in understanding $^{210}Pb$ activity profiles. These postdepositional processes include bioturbation, erosion by wave and current action, and gas generation. Few environments are completely undisturbed by postdepositional mixing of some type, and these processes must be considered when studying rates of sediment accumulation.

Recently, several studies have been conducted involving assessment of the influence of bioturbation on sedimentological records (Davis, 1974; Guinasso and Schink, 1975; Peng and Broecker, 1979; DeMaster and Cochran, 1977). Bioturbation can influence accumulation rates derived from radiometric dating techniques in areas in which sediment accumulation is slow and the degree of reworking of the sediment column is intense. However, in environments of rapid accumulation or those having a minimum of biological sediment mixing, the influence is small.

X-radiography shows that only core 3, taken in Howard Bay, contains a sufficient number of worm burrows to cause concern for bioturbation or mixing which reflects burrowing and feeding activities. These burrows are in the top 20 cm of the core and they probably account for the constant $^{210}Pb$ activity observed there. The other cores show a similar zone of constant $^{210}Pb$ activity below the sediment-water interface, ranging in thickness from 5-20 cm, which is not explained by bioturbation. This zone may be due to wave and current agitation, or to a mechanism reported by Gahler (1969) which involved the formation of gas pockets and the resuspension of sediments.

Bond, Hazel, and Vincent (1968) discussed the effect of wind on the resuspension of bottom sediments in the overlying waters. They concluded that sediments were resuspended when the water mass movement had a velocity greater than 0.02 ft/sec and that this water velocity occurred when the wind velocities were 2-5 mph. Wind-induced currents could cause mixing and erosion because of the loose nature of the lakebed sediments. Similar water movement could be caused by the activities of motorboats in the area.

The mechanisms described by Gahler (1969) to explain the increase in nutrients in the water also could explain the mixing noted in the tops of several cores. *Oscillatoria princeps*, an alga which forms on the bottom sediment at certain times of the year, collects sufficient gas to cause it to be lifted to the lake surface along with attached sediment. These chunks of sediment, up to 30 cm long and 15-30 cm thick, have been found floating in the lake. Although it is not known how long this

mechanism has occurred in Upper Klamath Lake, *Oscillatoria* and other decomposing algae are reported to have caused a very disagreeable odor in the bay for many years.

### Trace Metals

Water enters Upper Klamath Lake from mountain streams, rivers, irrigation canals, springs, agricultural drainage, and by precipitation. Agricultural runoff, primarily in the early spring, is yellow in color and suspect to some type of contamination (Miller and Tash, 1967). Previously reported trace metal values for surface-sediment samples are: Cd–14 ppm, Cu–4 ppm, Fe–11,400 ppm, Pb–14 ppm, Mn–183 ppm, and Zn–14 ppm (Miller and Tash, 1967). The cores from this study were analyzed for the same metals and chromium to establish baseline values and to compare recent surface concentrations with stratigraphic distributions of these metals. Trace-metal concentrations for the upper 30 cm are presented in Table 2. Detailed concentrations with depth are given in Martin and Rice (1980). Results show that concentrations of these metals are lower than values reported for other lakes, especially for lakes which receive large amounts of industrial waste, municipal sewage, and other contaminants (Nriagu *et al.*, 1979; Edgington and Robbins, 1976). Values for Cd, Fe, Pb, and Mn in this report are lower, and concentrations for Cu and Zn are higher than those reported by Miller and Tash (1967). Concentrations of all metals except Cu in the core from Lake Euwana are higher than values from any Upper Klamath Lake Core; copper values are about the same. No reason for this enrichment is readily apparent. All the cores from Upper Klamath Lake show increases in lead concentrations toward the surface. These increases may be attributed to increased cultural activities during the past 100-150 years and were probably added through atmospheric fallout; the atmosphere is now widely recognized as a major source of metal pollution in lacustrine environments (Nriagu *et al.*, 1979). Six cores show an increase in manganese in the upper layers. The most likely explanation for this enrichment is the migration of soluble $Mn^{+2}$ from lower portions of the sediment column. The lake sediments are composed of large amounts of organic material. As this material decays at depths, it produces a reducing environment. Manganese is reduced to a soluble species which migrates upward by ionic diffusion through the pore water until it reaches an area of oxidation near the sediment surface. There, it is reprecipitated as an oxide, resulting in an enrichment of Mn in the top portion of the core. Such remobilization of Mn has been documented by other investigators (Lynn and Bonatti, 1965; Thomson *et al.*, 1975).

### Sedimentation Rates

Sedimentation rates calculated from $^{210}Pb$ activities indicate that the lakes are accumulating sediment at an average rate of 3.0 mm/yr. The sedimentation rates for individual cores are presented in Table 1. The sediments of these lakes are relatively homogenous; however, the upper portion of each core has a slightly higher water content than the rest of the core. Because of this compaction in the lower portion of the core, the sedimentation rate expressed as centimeters per year can change over the length of the core even though the amount of sediment deposited each year is relatively constant. To eliminate the influence of water content, each sample interval was normalized to the lowest water content observed in the core. These new intervals were restacked and a rate was calculated for the compacted core. Plots of excess $^{210}Pb$ activity (disintegration/minute/gram) versus compacted core depth are shown in Figure

TABLE 2. Trace metal concentrations in parts per million (ppm) in the upper 30 cm of sediment. See Fig. 1 for core locations.

| Core | Cadmium | | Chromium | | Copper | | Iron | | Manganese | | Lead | | Zinc | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range |
| 1 | 0.03 | 0.01-0.06 | 20.3 | 16.2-30.4 | 11.0 | 6.5-19.9 | 10,000 | 7,400-18,000 | 11.1 | 7.0-22.5 | 1.9 | 0.9-3.0 | 20.1 | 16.1-26.5 |
| 2 | 0.05 | 0.03-0.09 | 20.3 | 16.4-24.4 | 12.3 | 8.4-21.6 | 10,800 | 8,500-12,100 | 24.8 | 12.3-24.8 | 4.9 | 2.4-9.9 | 23.5 | 18.6-28.8 |
| 3 | 0.04 | 0.01-0.12 | ND | ND | 14.8 | 7.8-46.2 | 11,900 | 6,800-14,700 | 12.9 | 6.7-27.7 | 2.6 | 0.9-6.2 | 20.2 | 14.6-24.6 |
| 4 | 0.05 | 0.04-0.08 | ND | ND | 14.5 | 10.3-21.1 | 9,100 | 6,400-11,200 | 63.9 | 22.6-244.7 | 4.5 | 2.7-10.4 | 23.1 | 16.7-25.8 |
| 5 | 0.04 | 0.03-0.06 | ND | ND | 10.0 | 7.2-12.3 | 12,800 | 9,500-15,900 | 46.6 | 20.1-82.0 | 2.7 | 1.8-5.3 | 22.9 | 16.2-31.9 |
| 6 | 0.04 | 0.01-0.10 | 32.3 | 15.7-56.1 | 8.8 | 2.8-15.3 | 5,600 | 2,400-12,700 | 23.7 | 15.0-37.2 | 2.2 | 0.2-5.1 | 4.9 | 2.3-8.4 |
| 7 | 0.12 | 0.03-0.25 | ND | ND | 19.1 | 13.0-21.8 | 14,900 | 9,900-17,900 | 36.4 | 16.7-54.7 | 14.9 | 2.9-20.3 | 45.9 | 16.0-57.5 |
| 8 | 0.04 | 0.02-0.10 | ND | ND | 14.9 | 10.3-23.0 | 10,700 | 8,300-11,500 | 36.0 | 26.5-40.6 | 3.7 | 2.0-5.3 | 21.3 | 16.2-57.5 |
| 9 | 0.04 | 0.02-0.06 | 29.9 | 23.0-34.6 | 10.8 | 8.2-15.3 | 10,000 | 6,800-12,100 | 48.8 | 23.3-129.6 | 1.8 | 0.4-4.0 | 5.6 | 3.7-7.5 |
| % deviation of replicate analyses | 4.6 | | 6.0 | | 5.3 | | 4.7 | | 2.2 | | 5.4 | | 4.3 | |

ND = not determined

2. The background activity ($^{226}$Ra-supported $^{210}$Pb activity) used to calculate the excess $^{210}$Pb activity was 0.4 dpm/g. Some of the cores were not long enough to determine the background activity; for these cores, the average background activity of 0.4 dpm/g was assumed. Data from the sediment mixing layers which showed constant $^{210}$Pb activity were not used in the rate calculations. The amount of sediment deposited per unit surface area per unit time was also calculated for each core, assuming a grain density of 2.5 g/cm$^3$ for the dried solids and 1.0 g/cm$^3$ for the pore water. This accumulation rate is expressed by the following relationship using the sedimentation rate of the compacted core and the lowest water content observed in the core.

$$R = (1 - C_w)\ sr$$

where $R$ = rate expressed as g/cm$^2$/yr
$C_w$ = lowest water content observed
$s$ = particle density
$r$ = rate expressed as cm/yr

The accumulation rate ranged from 0.03 g/cm$^2$/yr at site 3 to 0.48 g/cm$^2$/yr at site 4.

Sedimentation rates determined in Upper Klamath Lake and Lake Euwana are the same order of magnitude as rates reported for other lacustrine environments (Koide *et al.*, 1973; Nriagu *et al.*, 1979; Robbins and Edgington, 1975). Sedimentation rates in most lakes range from fractions of a millimeter to several centimeters per year. The highest rate of sedimentation, 8.5 mm/yr (0.48 g/cm$^2$/yr) was determined in core 4, which was retrieved near the input from Agency Lake. The lowest recent accumulation rate, 0.9 mm/yr (0.03 g/cm$^2$/yr) was found in core 3 taken in Howard Bay, a shallow body of water which receives agricultural runoff (usually once a year) and is not as influenced as the main part of the lake by inflow and outflow. Two rates are reported for core 6 (Fig. 2) because there was a distinct change in the $^{210}$Pb activity pattern. This change may be caused by a change in sedimentation reflecting changes in land use in the watershed area. It may also be the result of the influence of the sediment mixing layer and high moisture content of the lake sediments on the distribution of $^{210}$Pb in the cores. The activity profile for core 6 also shows an 8 cm layer, at a depth of 12-14 cm, that appears to have been deposited as a single event rather than as a continuous accumulation of sediment. The location of the core with respect to the outflow from the Williamson River indicates that this layer may be an episodic deposit from the river during a time of high-energy discharge to the lake. If we assume a rate of 1.9 mm/yr, this layer would correspond to about 1905. Core 8 shows an unusual activity profile; it shows an area of constant $^{210}$Pb activity followed by a sharp drop in activity followed by a normal decay curve (Fig. 2). This core was obtained on a slope and some type of mass movement such as slumping could be responsible for the unusual profile. Gahler and Sanville (1971) reported that, based on radiocarbon dating of a core taken near the outlet from Upper Klamath Lake, 3000 years were required to deposit a 15 cm layer of sediment between the 60 cm and 90 cm levels; but that only about 100 years were required to deposit a 15 cm layer between 30 cm and 60 cm (about 1.5 mm/yr). The rate obtained from core 1 of this study taken near the outlet from Upper Klamath Lake was determined by $^{210}$Pb dating to be 1.8 mm/yr which is in excellent agreement with Gahler and Sanville's

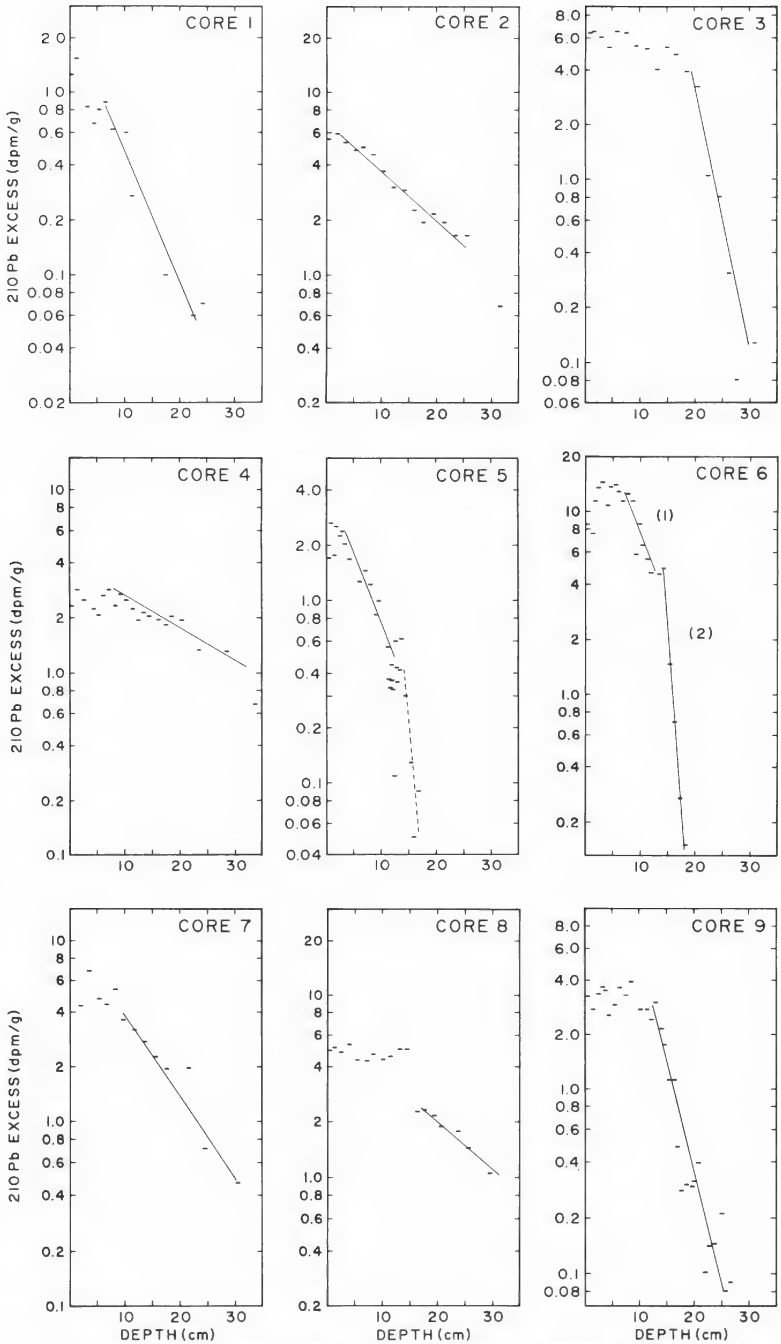


Figure 2. Excess $^{210}Pb$ activities (dpm/g) versus compaction corrected depths (cm). The calculated sediment rates are presented in Table 1.

rate obtained between 30 and 60 cm. If the rate has changed significantly, the data reported by Gahler and Sanville may reflect the recent rate indicative of the past 100-200 years as well as the slower historical rate.

#### Summary

1. Sedimentation rates based on $^{210}Pb$ show that Upper Klamath Lake and Lake Euwana are filling at approximately 3.0 mm/yr. If sediment continues to accumulate at the present rate, there is no immediate threat to economically important activities supported by the lake;

2. Trace metal concentrations in sediments from Lake Euwana are generally higher than concentrations in sediments from Upper Klamath Lake. However, all of the cores analyzed showed very low concentrations of these metals when compared with most lacustrine environments;

3. The sediments from the lakes except for a few pumice layers are relatively homogeneous in texture and in moisture content (81-92 percent); and

4. There is a sediment mixing layer ranging from 5-20 cm in depth throughout most of the lake due to bioturbation, wave-current action, and gas generation.

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# Food Habits of Eastern Oregon Bats, Based on Stomach and Scat Analyses

**Abstract**

The diets of 12 species of bats were analyzed through examination of 413 stomachs and 536 scats. Results from scat analysis were compared to those from stomach analysis, and some differences were discerned. For example, lepidopterans were somewhat overrepresented and homopterans were somewhat underrepresented in scats; overall, however, scat analysis was deemed to be acceptable and was fairly indicative of the food intake in the following species of bats: *Myotis lucifugus, M. yumanensis, M. evotis, M. volans, M. californicus, M. leibi, Antrozous pallidus, Eptesicus fuscus, Lasionycteris noctivagans, Pipistrellus hesperus,* and *Plecotus townsendi.*

## Introduction

Whitaker *et al.* (1977) presented information on the food habits of western Oregon bats, and Whitaker *et al.* (1981) summarized information on the food habits of *Lasionycteris noctivagans* in Oregon. No information is available, however, on the food habits of other species of bats from eastern Oregon. In fact, little information occurs anywhere on the food habits of *Myotis evotis, M. volans,* and *Pipistrellus hesperus.*

Stomach analysis has been considered better than scat analysis to assess the food habits of most vertebrates, particularly insectivores and predators. Because of differential digestion, softer items digest faster and are thus completely gone or underrepresented in scats, as compared to stomachs.

Insectivorous bats were thought to be an exception, however, because they feed essentially on insects that contain relatively indigestible chiton. Merlin Tuttle (in prep.) has shown that certain foods, particularly mayflies (Emphemeraptera), may not show up in bat scat samples. Part of the reason, in this case, was rapid passage through a digestive tract. Bats apparently voided their intestines of mayflies and picked up new foods while returning to their roosts. In addition, mayflies were found to digest more rapidly than other food items.

The purpose of this paper is two-fold: first, to present food-habit data for the bats of eastern Oregon; and second, to supplement stomach analysis with scat analysis in order to evaluate the latter as a technique for food habit studies. Scat analysis is desirable because bats could be collected, held until they defecated, and then released. If scat analysis is reliable, then the food habits of rare, threatened, or endangered species could be studied without having to sacrifice individuals.

## Study Area

Bats were collected in Baker, Grant, Harney, Malheur, Union, and Wallowa Counties. The habitats fell within the following major vegetation areas: *Pinus ponderosa* Zone (broad sense), *Abies grandis* Zone, *Pseudotsuga menziesii* Zone, Steppe (without *Artemisia tridentata*), Shrub-steppe (with *A. tridentata*), Desert Shrub, and *Juniperus occidentalis* Zone (Franklin and Dyrness, 1973). These habitats are in the Blue Mountains, High Lava Plains, Basin and Range, and Owyhee Upland physiographic provinces (Franklin and Dyrness, 1973).

## Methods and Materials

Bats were collected from 1975 through 1978 primarily in mistnets, but some were shot. The mistnetted bats used for stomach analysis were killed immediately; those used for scat analysis were immediately placed into paper cups, allowed to defecate, then released. All scat samples came from Grant County.

Both stomach contents and scats were preserved in 10 percent formalin. They were examined and estimates were made of the percentage volume of each food in each stomach and scat sample by visual observation using a 10- to 70-power zoom dissecting microscope.

## Results and Discussion

Results of the stomach analysis are given in Tables 1 and 2, and those of the scat analysis are given in Tables 3 and 4. Table 5 presents summary of results by insect orders and compares stomach and scat analyses.

Ideally, one should have both stomachs and scats taken from bats at the same time and locality when making a comparative analysis of their contents. Such was not the case in this study; scat samples were all from Grant County, whereas stomach samples, of necessity, were from several counties. Nevertheless, we thought some valid comparative data could be gained because there often is considerable general similarity in food habits of insectivorous bats within species and among localities and times.

### Habitat Considerations

*Myotis lucifugus*, little brown myotis. The distribution of *Myotis lucifugus* was spotty throughout Oregon. Where they occurred in forested areas, they tended to feed along the edge of the forest. In rangelands, however, they foraged primarily over water.

*Myotis yumanensis*, Yuma myotis. Exceedingly scarce in eastern Oregon, *Myotis yumanensis* was captured only in Grant County. Nothing was observed of its feeding habits.

*Myotis evotis*, long-eared myotis. *Myotis evotis* proved to be the most widely

TABLE 1. Foods eaten by six species of bats of the genus **Myotis** from eastern Oregon, as indicated by stomach analysis.

| | **M. lucifugus** | | **M. yumanensis** | | **M. evotis** | | **M. volans** | | **M. californicus** | | **M. leibi** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq |
| N = | 28 | | 7 | | 121 | | 90 | | 28 | | 6 | |
| Lepidoptera (moths) | 21.8 | 46.4 | 22.9 | 57.1 | 53.7 | 81.8 | 58.6 | 83.3 | 84.3 | 92.9 | 65.0 | 83.3 |
| Isoptera (termites) | 3.2 | 3.6 | 12.9 | 42.9 | 0.1 | 0.8 | | | | | | |
| Diptera (flies) | | | | | | | | | | | | |
| Chironomidae | 14.7 | 25.0 | 2.9 | 14.3 | 0.3 | 3.3 | 0.2 | 2.2 | 2.7 | 3.6 | | |
| Chirinomid pupae | 1.1 | 7.1 | | | | | | | | | | |
| Lonchopteridae | 3.9 | 14.3 | | | | | | | | | | |
| Tipulidae | | | | | | | 0.7 | 2.2 | 0.9 | 3.6 | | |
| Rhagionidae | | | | | 0.1 | 0.8 | 0.1 | 1.1 | | | | |
| Syrphidae | | | | | | | 0.2 | 1.1 | | | | |
| Unidentified | 17.1 | 16.7 | 7.1 | 57.1 | 8.3 | 34.7 | 7.2 | 26.7 | 6.8 | 17.9 | 12.5 | 33.3 |
| Hymenoptera (bees & wasps) | | | | | | | | | | | | |
| Formicidae | 3.0 | 3.6 | | | 1.1 | 3.3 | | | | | | |
| Halictidae | | | | | | | 0.2 | 1.1 | | | | |
| Unidentified | 0.9 | 7.1 | | | 0.9 | 3.3 | 0.2 | 1.1 | | | 0.8 | 16.7 |
| Hemiptera (bugs) | | | | | | | | | | | | |
| Pentatomidae | | | | | | | | | | | | |
| Lygaeidae | 3.0 | 3.6 | | | 2.2 | 8.3 | 5.2 | 21.1 | 1.1 | 10.7 | 7.5 | 16.7 |
| Neididae | | | | | 0.2 | 1.7 | | | | | | |
| Unidentified | 4.3 | 14.3 | | | 2.1 | 10.7 | 2.6 | 8.9 | 0.7 | 7.1 | 8.3 | 33.3 |
| Orthoptera (crickets) | | | | | | | | | | | | |
| Gryllidae | | | | | 0.2 | 1.7 | | | | | | |
| Trichoptera (caddis flies) | | | 13.6 | 14.3 | | | | | | | | |
| Coleoptera (beetles) | | | | | | | | | | | | |
| Scarabaeidae | 3.4 | 7.1 | | | 3.8 | 9.9 | 1.1 | 3.3 | 1.3 | 3.6 | 2.5 | 16.7 |
| Carabidae | | | | | 0.6 | 3.3 | 0.9 | 2.2 | 0.4 | 3.6 | | |
| Cerambycidae | | | | | 0.8 | 1.7 | 2.2 | 7.8 | | | | |
| Chrysomelidae | 2.9 | 3.6 | | | 0.3 | 2.5 | | | | | | |
| Alleculidae | | | | | 0.1 | 0.8 | | | | | | |
| Coccinellidae | | | | | 0.1 | 0.8 | | | | | | |
| Unidentified | 8.0 | 25.0 | 13.6 | 28.6 | 12.4 | 31.4 | 4.9 | 18.9 | 1.3 | 10.7 | | |
| Homoptera (leafhoppers) | | | | | | | | | | | | |
| Cicadelliadae | | | 13.6 | 28.6 | 1.3 | 5.8 | 1.5 | 8.9 | | | 2.5 | 16.7 |

TABLE 1. (Continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cercopidae | 2.9 | 3.6 | | | 3.7 | 12.4 | 11.4 | 37.8 | | | | |
| Delphacidae | 0.2 | 7.1 | | | 0.2 | 1.7 | 0.3 | 2.2 | | | | |
| Unidentified | 0.2 | 3.6 | | | 0.7 | 5.8 | | | | | | |
| Arachnida (spiders) | | | | | | | | | | | | |
| Araneida | | | | | 1.2 | 3.3 | | | | | | |
| Neuroptera (lacewings) | | | | | | | | | | | | |
| Hemerobiidae | 0.7 | 3.6 | | | 2.8 | 8.3 | | | | | | |
| Unidentified Insects | 3.6 | 21.4 | 13.6 | 57.1 | 2.7 | 14.9 | 2.4 | 12.2 | 0.7 | 7.1 | 0.8 | 16.7 |
| Chilopoda (centipedes) | | | | | 0.1 | 0.8 | | | | | | |
| Phalangida (harvestmen) | | | | | 0.4 | 0.8 | | | | | | |
| Unidentified Invertebrates | 3.6 | 21.4 | | | | | | | | | | |
| | 98.5 | | 100.2 | | 100 | | 99.9 | | 100.2 | | 99.9 | |

TABLE 2. Foods eaten by five species of bats from eastern Oregon, as indicated by stomach analysis.

| | Antrozous pallidus | | Eptesicus fuscus | | Lasionycteris noctivagans | | Pipistrellus hesperpus | | Plecotus Townsendi | |
|---|---|---|---|---|---|---|---|---|---|---|
| | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq |
| n = | 5 | | 60 | | 41 | | 26 | | 1 | |
| Lepidoptera (moths) | 20.0 | 20.0 | 13.8 | 30.0 | 29.7 | 51.2 | 15.9 | 46.2 | 100 | 100 |
| Isoptera (termites) | | | 0.3 | 3.3 | | | | | | |
| Diptera (flies) | | | | | | | | | | |
| Chironomidae | | | | | 0.1 | 2.4 | 5.2 | 23.1 | | |
| Tipulidae | | | | | | | 0.8 | 3.8 | | |
| Muscoidea | | | 0.2 | 1.7 | | | 0.8 | 3.8 | | |
| Unidentified | | | 1.5 | 15.0 | 10.9 | 39.0 | 24.8 | 84.6 | | |
| Hymenoptera (bees & wasps) | | | | | | | | | | |
| Formicidae | | | 9.2 | 18.3 | 12.2 | 31.7 | 8.8 | 11.5 | | |
| Ichneumonidae | | | | | | | 1.7 | 3.8 | | |
| Cynipoidea-Chalcidoidea | | | | | | | 0.9 | 7.7 | | |
| Unidentified | | | | | | | 11.2 | 30.8 | | |
| Hemiptera (bugs) | | | | | | | | | | |
| Pentatomidae | | | 1.0 | 8.3 | | | 1.2 | 3.8 | | |
| Lygaeidae | | | 2.9 | 21.7 | 1.7 | 2.4 | 2.9 | 11.5 | | |
| Neididae | | | 0.2 | 1.7 | | | | | | |
| Miridae | | | 0.3 | 1.7 | | | 3.3 | 7.7 | | |
| Unidentified | | | 1.9 | 13.3 | 6.2 | 36.6 | 3.5 | 19.2 | | |
| Orthoptera (crickets) | | | | | | | | | | |
| Gryllidae | | | 0.3 | 1.7 | | | | | | |
| Unidentified | 60.0 | 60.0 | 0.6 | 3.3 | | | | | | |
| Trichoptera (caddis flies) | | | 0.5 | 1.7 | 1.1 | 2.4 | | | | |
| Coleoptera (beetles) | | | | | | | | | | |
| Scarabaeidae | | | 22.7 | 40.0 | 0.9 | 4.9 | | | | |
| Carabidae | | | 11.9 | 18.3 | 0.1 | 2.4 | | | | |
| Cerambycidae | | | 2.3 | 11.7 | | | | | | |
| Chrysomelidae | | | 2.5 | 5.0 | 1.3 | 4.9 | | | | |
| Nitidulidae | | | | | | | 0.9 | 3.8 | | |
| Unidentified | | | 13.2 | 35.0 | 8.4 | 41.5 | 3.4 | 23.1 | | |
| Homoptera (leafhoppers) | | | | | | | | | | |
| Cicadelliadae | | | 0.3 | 8.3 | 1.7 | 14.6 | 2.1 | 11.5 | | |
| Cercopidae | | | 9.9 | 21.7 | 22.7 | 43.9 | 0.4 | 3.8 | | |
| Delphacidoe | | | | | | | 1.9 | 7.7 | | |
| Fulgoridae | | | | | 0.1 | 2.4 | | | | |
| Unidentified | | | | | | | 0.8 | 3.8 | | |
| Arachnida (spiders) | | | | | | | | | | |
| Araneida | | | 0.1 | 1.7 | | | | | | |
| Neuroptera (lacewings) | | | | | | | | | | |
| Hemerobiidae | | | 1.3 | 11.7 | 0.5 | 7.3 | 1.2 | 7.7 | | |
| Unidentified Insects | 20.0 | 20.0 | 2.8 | 20.0 | 2.4 | 17.1 | 9.0 | 34.6 | | |
| Phalangida (harvestmen) | | | 0.3 | 1.7 | | | | | | |
| | 100 | | 100 | | 100 | | 99.9 | | 100 | |

distributed bat in eastern Oregon and the most abundant bat in northeastern Oregon forests. (Care must be taken in identifying them, however, because a high proportion tend to have readily visible fringes on the uropygium that are reminiscent of *Myotis thysanodes.*)

*Myotis volans*, long-legged myotis. *Myotis volans* was the second most abundant bat in forests of northeastern Oregon and often the first to feed, usually among the trees. They were not found, however, in the arid rangelands of southeastern Oregon.

*Myotis californicus*, California myotis. *Myotis californicus*, although widely distributed throughout eastern Oregon, was nowhere easily collected.

TABLE 3. Foods eaten by six species of bats of the genus **Myotis** from eastern Oregon, as indicated by scat analysis.

| | **M. lucifugus** | | **M. yumanensis** | | **M. evotis** | | **M. volans** | | **M. californicus** | | **M. thysanodes** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq | vol | freq |
| n = | 3 | | 4 | | 69 | | 139 | | 64 | | 4 | |
| Lepidoptera (moth) | 73.3 | 100.0 | 33.8 | 50.0 | 58.6 | 82.6 | 77.8 | 97.1 | 51.9 | 90.6 | 42.5 | 75.0 |
| Larvae | | | | | | | 0.1 | 0.7 | 0.1 | 1.6 | | |
| Isoptera (termites) | | | | | 0.3 | 1.4 | 0.1 | 0.7 | 0.7 | 6.3 | | |
| Diptera (flies) | | | | | | | | | | | | |
| Larvae | | | | | | | 0.04 | 0.7 | | | | |
| Chironomidae | | | 8.8 | 25.0 | | | 0.7 | 4.3 | | | | |
| Tipulidae | | | | | 0.2 | 1.4 | 0.1 | 1.4 | 2.9 | 7.8 | | |
| Muscoidea | | | | | | | 0.4 | 0.7 | 1.2 | 3.1 | | |
| Mycetophilidae | | | | | 0.2 | 1.4 | | | | | | |
| Unidentified | 11.7 | 66.7 | 12.5 | 75.0 | 10.8 | 43.5 | 5.7 | 28.1 | 14.3 | 68.8 | 7.5 | 50.0 |
| Hymenoptera (bees & wasps) | | | | | | | | | | | | |
| Formicidae | | | 2.5 | 25.0 | 0.7 | 4.3 | 0.9 | 5.0 | 0.1 | 1.6 | | |
| Cynipoidae | | | | | 0.1 | 1.4 | 0.1 | 1.4 | | | | |
| Vespidae | | | | | | | 0.2 | 0.7 | 0.9 | 1.6 | | |
| Unidentified | | | | | 0.7 | 4.3 | 0.9 | 2.2 | 0.2 | 1.6 | | |
| Hemiptera (bugs) | | | | | | | | | | | | |
| Lygaeidae | 3.3 | 33.3 | | | 3.2 | 10.1 | 0.9 | 9.4 | 1.2 | 7.8 | | |
| Nabidae | | | | | | | 0.1 | 0.7 | | | | |
| Miridae | | | | | 0.5 | 2.9 | | | 0.4 | 3.1 | 2.5 | 25.0 |
| Unidentified | | | | | 1.2 | 7.2 | 0.2 | 2.2 | 0.2 | 3.1 | | |
| Orthoptera (crickets) | | | | | | | | | | | | |
| Gryllidae | | | | | | | 0.1 | 0.7 | | | | |
| Coleoptera (beetles) | | | | | | | | | | | | |
| Scarabaeidae | | | | | | | 0.4 | 2.2 | 0.2 | 1.6 | | |
| Carabidae | | | | | 1.0 | 4.3 | 0.3 | 1.4 | | | | |
| Tenebrionidae | | | | | 0.1 | 1.4 | 0.3 | 0.7 | | | | |
| Chrysomelidae | | | | | 0.4 | 1.4 | 0.3 | 0.7 | 0.7 | 1.6 | | |
| Unidentified | | | 12.5 | 50.0 | 4.6 | 17.4 | 3.4 | 16.5 | 6.4 | 29.7 | | |
| Larvae | | | | | | | | | 0.5 | 1.6 | | |
| Homoptera (leafhoppers) | | | | | | | | | | | | |
| Cicadellidae | | | | | 1.9 | 8.7 | 0.6 | 7.9 | 3.1 | 9.4 | | |
| Cercopidae | | | | | 0.1 | 1.4 | 0.1 | 0.7 | 1.1 | 4.7 | | |
| Fulgoridae | | | 7.5 | 25.0 | | | | | 0.1 | 1.6 | 17.5 | 50.0 |

TABLE 3. (Continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Aphidoidea | | | | | | | 0.1 | 1.4 | | | | |
| Membracidae | | | | | | | 0.1 | 0.7 | | | | |
| Unidentified | 5.0 | 33.0 | | | | | 0.1 | 0.7 | 0.4 | 3.1 | | |
| Arachnida (spiders) | | | | | | | | | | | | |
| Araneida | | | | | 1.3 | 2.9 | 0.1 | 0.7 | | | | |
| Acarina | | | | | | | 0.01 | 0.7 | | | | |
| Neuroptera (lacewings) | | | | | | | | | | | | |
| Hemeroblidae | 6.7 | 33.3 | 5.0 | 50.0 | 4.8 | 23.2 | 3.5 | 19.4 | 9.5 | 32.8 | 7.5 | 25.0 |
| Chrysopidae | | | | | 0.1 | 1.4 | | | | | | |
| Unidentified Insects | | | 13.8 | 75.0 | 6.2 | 21.7 | 1.9 | 12.2 | 3.9 | 18.8 | 22.5 | 25.0 |
| Vegetation | | | | | 2.9 | 10.1 | 0.7 | 5.0 | | | | |
| Grass Seeds | | | | | | | 0.01 | 0.7 | | | | |
| Unidentified Larvae | | | 3.8 | 25.0 | | | | | | | | |
| | 100 | | 100.2 | | 99.8 | | 100.2 | | 100 | | 100 | |

*Myotis leibi*, small-footed myotis. A bat of the arid rangelands, Bailey (1936) indicated that it was a rather abundant species. *Myotis leibi* proved to be difficult to secure, however, even though it was an early flier, foraging back and forth along cliffs.

*Myotis thysanodes*, fringed myotis. *Myotis thysanodes* is either an uncommon bat in eastern Oregon or is difficult to collect. Regardless, almost nothing is known about it within the state.

*Antrozous pallidus*, pallid bat. Although *Antrozous pallidus* was not often collected during our study, the species was much more common in eastern Oregon than our records indicate. This bat foraged low to the ground along cliffs and over lava flows,

TABLE 4. Foods eaten by three species of bats from eastern Oregon, as indicated by scat analysis.

| | **Eptesicus fuscus** | | **Lasionycteris noctivagans** | | **Lasiurus cinereus** | |
|---|---|---|---|---|---|---|
| | vol | freq | vol | freq | vol | freq |
| n = | 177 | | 70 | | 6 | |
| Lepidoptera (moths) | 24.1 | 63.8 | 64.4 | 95.7 | 98.3 | 100.0 |
| Isoptera (termites) | 0.6 | 3.9 | 0.8 | 4.3 | | |
| Diptera (flies) | | | | | | |
| Tipulidae | 2.1 | 14.1 | 5.1 | 24.3 | | |
| Muscoidea | | | 0.1 | 1.4 | | |
| Otitidae | | | 0.03 | 1.4 | | |
| Unidentified | 5.9 | 42.9 | 4.6 | 40.0 | 0.8 | 16.7 |
| Hymenoptera (bees & wasps) | | | | | | |
| Formicidae | 2.0 | 5.6 | 0.8 | 10 | | |
| Ichneumonidae | 0.2 | 1.1 | | | | |
| Unidentified | 0.3 | 3.9 | 0.4 | 1.4 | | |
| Hemiptera (bugs) | | | | | | |
| Pentatomidae | 0.3 | 2.3 | | | | |
| Lygaeidae | 4.1 | 29.9 | 1.4 | 12.9 | | |
| Coreidae | 0.1 | 1.1 | 0.1 | 1.4 | | |
| Miridae | 1.4 | 6.8 | 0.5 | 2.9 | | |
| Unidentified | 0.5 | 3.4 | 2.1 | 15.7 | | |
| Orthoptera (crickets) | | | | | | |
| Gryllidae | | | 2.1 | 4.3 | | |
| Trichoptera (caddis flies) | 0.8 | 6.8 | | | | |
| Coleoptera (beetles) | | | | | | |
| Lathridiidae | 0.03 | 0.6 | | | | |
| Scarabaeidae | 26.7 | 46.3 | 0.1 | 1.4 | | |
| Carabidae | 2.6 | 5.1 | | | | |
| Cerambycidae | 1.6 | 3.9 | | | | |
| Chrysomelidae | 0.1 | 0.6 | 0.2 | 1.4 | | |
| Alleculidae | 0.03 | 0.6 | | | | |
| Curculionidae | 0.2 | 0.6 | | | | |
| Tenebrionidae | 0.3 | 1.7 | | | | |
| Unidentified | 6.2 | 28.2 | 1.3 | 12.9 | | |
| Homoptera (leafhoppers) | | | | | | |
| Cicadellidae | 2.9 | 16.9 | 1.2 | 4.3 | | |
| Cercopidae | 6.8 | 25.4 | | | | |
| Unidentified | 0.1 | 0.6 | 1.4 | 7.1 | | |
| Neuroptera (lacewings) | | | | | | |
| Hemerobiidae | 5.5 | 31.6 | 9.8 | 30.0 | | |
| Unidentified | | | 0.1 | 1.4 | | |
| Unidentified Insects | 4.0 | 24.3 | 1.6 | 7.1 | 0.3 | 16.7 |
| Arachnida (spiders) | | | | | | |
| Araneida | | | 0.07 | 1.4 | | |
| Acarina | 0.02 | 1.7 | | | | |
| Vegetation | 0.6 | 4.5 | 1.9 | 2.9 | 0.5 | 16.7 |
| | 100 | | 100.1 | | 99.9 | |

TABLE 5. Summary, by insect orders, of food habits data of eastern Oregon bats, as indicated by stomach vs. scat analysis.

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lepidotera | Stomach | 21.8 | 22.9 | 53.7 | 58.6 | 84.3 | 65.0 | * | 20.0 | 13.8 | 29.7 | * | 15.9 | 100.0 |
| | Scat | 73.3 | 33.8 | 58.6 | 77.8 | 51.9 | * | 42.5 | * | 24.1 | 64.4 | 98.3 | * | * |
| Diptera | Stomach | 37.8 | 10.0 | 8.7 | 8.4 | 10.4 | 12.5 | * | — | 1.7 | 11.0 | * | 30.8 | — |
| | Scat | 11.7 | 21.3 | 11.2 | 6.9 | 18.4 | * | 7.5 | — | 8.0 | 9.8 | 0.8 | * | — |
| Hemiptera | Stomach | 7.3 | — | 4.5 | 7.8 | 1.8 | 15.8 | * | — | 6.3 | 7.9 | — | 10.9 | — |
| | Scat | — | — | — | 1.3 | 1.8 | * | 2.5 | — | 6.4 | 4.1 | — | * | — |
| Coleoptera | Stomach | 14.3 | 13.6 | 18.1 | 9.1 | 3.0 | — | — | — | 52.6 | 10.7 | — | 4.3 | — |
| | Scat | 0.0 | 12.5 | 6.1 | 4.7 | 7.8 | — | — | — | 37.8 | 1.6 | — | * | — |
| Homoptera | Stomach | 3.8 | 13.6 | 5.9 | 13.2 | — | 2.5 | * | — | 10.2 | 24.5 | — | 5.2 | — |
| | Scat | 5.0 | 7.5 | 2.0 | 1.0 | 4.7 | * | 17.5 | — | 11.8 | 2.6 | — | * | — |
| Orthoptera | Stomach | — | — | 0.2 | — | — | — | — | 60.0 | 0.3 | — | — | — | — |
| | Scat | — | — | 4.0 | 0.1 | — | — | — | * | — | 2.1 | — | — | — |
| Isoptera | Stomach | — | 12.9 | 0.1 | — | — | — | — | — | 0.3 | 3.2 | — | — | — |
| | Scat | — | — | 0.3 | 0.1 | 0.7 | — | — | — | 0.6 | 0.8 | — | — | — |
| Hymenoptera | Stomach | 3.9 | — | 2.0 | 0.4 | — | 0.8 | — | — | 9.2 | 12.2 | — | 21.7 | — |
| | Scat | — | — | 2.1 | 2.1 | 1.2 | * | — | — | 2.5 | 1.2 | — | * | — |
| Trichoptera | Stomach | — | 13.6 | — | — | — | — | — | — | 0.5 | 1.1 | — | — | — |
| | Scat | — | — | — | — | — | — | — | — | 0.8 | — | — | — | — |
| Neuroptera | Stomach | 0.7 | — | 2.8 | — | — | — | * | — | 1.3 | 0.5 | — | 1.2 | — |
| | Scat | 6.7 | 5.0 | 4.9 | 3.5 | 9.5 | — | 7.5 | — | 5.5 | 9.8 | — | * | — |

* = no scats or no stomachs examined from this species.

usually making it difficult to net. In addition, it normally took wing after it was too dark to shoot accurately.

*Eptesicus fuscus*, big brown bat. *Eptesicus fuscus* was widely distributed, but appeared to be more common in the forests of northeastern Oregon than it did in the southeastern rangelands. This large, adaptable bat fed over the forest canopy, along roads through the trees, along the forest edge, over forest clearings, and along cliffs and canyon streams.

*Lasionycteris noctivagans*, silver-haired bat. *Lasionycteris noctivagans* is primarily a forest bat, but it also inhabits the juniper woodlands of southeastern Oregon. It can be found throughout the rangelands, however, when it migrates in May and September. This bat is an early flier. It forages over the forest canopy, along roads through the trees, and along the forest edge. During migration, it also feeds back and forth along rangeland streams that have good riparian vegetation.

*Lasiurus cinereus*, hoary bat. *Lasiurus cinereus* is generally distributed throughout the forested areas of eastern Oregon, and is occasionally found in the arid rangelands during its spring and fall migrations. The swiftest bat in eastern Oregon, it normally flies well after dark. It feeds above the forest canopy, along roads through the trees, and over clearings.

*Pipistrellus hesperus*, western pipistrelle. The smallest Oregon bat, *Pipistrellus hesperus* inhabits the arid rangelands. This tiny bat is a crevice dweller and feeds in canyons, along cliffs, and over lava flows (Hayward and Cross, 1979; Maser *et al.*, 1979). It is also the first bat to become active in the evening.

*Plecotus townsendi*, western big-eared bat. Primarily a cave dweller in eastern Oregon, *Plecotus townsendi* is difficult to net. Although small numbers were found in lava tubes, their stomachs were empty. This bat flies well after dark and cannot be shot, and they are seldom caught in mistnets because they readily detect a net.

### Food Considerations

Food relationships among eastern Oregon bats (indicated only by orders of prey items at 10 percent or more of the volume in stomachs, except *Myotis thysanodes* and *Lasiurus cinereus* in which scats only were analyzed) were as follows:

*Lasiurus cinereus*—Lepidoptera
*Plecotus townsendi*—Lepidoptera
*Myotis evotis*—Lepidoptera-Coleoptera
*Myotis californicus*—Lepidoptera-Diptera
*Myotis volans*—Lepidoptera-Homoptera
*Myotis thysanodes*—Lepidoptera-Homoptera
*Myotis leibi*—Lepidoptera-Hemiptera-Diptera
*Lasionycteris noctivagans*—Lepidoptera-Homoptera-Hymenoptera-Diptera-Coleoptera
*Myotis yumanensis*—Lepidoptera-Coleoptera-Trichoptera-Homoptera-Isoptera-Diptera
*Myotis lucifugus*—Diptera-Lepidoptera-Coleoptera
*Pipistrellus hesperus*—Diptera-Hymenoptera-Lepidoptera-Hemiptera
*Eptesicus fuscus*—Coleoptera-Lepidoptera-Homoptera
*Antrozous pallidus*—Orthoptera-Lepidoptera

Of the nine species of bats that consume lepidopterans as their main food, only *Lasiurus cinereus* and *Plecotus townsendi* ate them exclusively. But the feeding habits of the two species are vastly different. *Lasiurus cinereus* is a fast flier and normally forages over the forest canopy and large openings within the forest, whereas *Plecotus townsendi* is probably the most versatile flier of the Oregon bats, and can forage in almost any habitat.

Four of the lepidopteran feeders had one other main food. *Myotis evotis* fed on coleopterans, and *Myotis californicus* ate dipterans. On the other hand, lepidopterans and homopterans were the main foods of both *Myotis volans* and *Myotis thysanodes*, but the latter is rarely encountered in eastern Oregon. In contrast, *Myotis leibi* had two main foods in addition to lepidopterans—hemipterans and dipterans.

*Lasionycteris noctivagans* and *Myotis yumanensis* were generalists; they ate three and five other major foods (respectively) in addition to lepidopterans. Further, *Myotis yumanensis* normally feeds near water whereas *Lasionycteris noctivagans* generally forages in any suitable habitat throughout the forest.

Two species (*Myotis lucifugus* and *Pipistrellus hesperus*) were primarily dipteran feeders. *Myotis lucifugus*, however, also ate lepidopterans and coleopterans, and *Pipistrellus hesperus* also consumed hymenopterans, lepidopterans, and hemipterans.

The last two species (*Eptesicus fuscus* and *Antrozous pallidus*) differed from all the others. *Eptesicus fuscus* ate coleopterans, lepidopterans, and homopterans; but *Antrozous pallidus* fed on orthopterans and lepidopterans.

### Comparison of Stomach and Scat Analyses

No isopterans or trichopterans showed up in *Myotis yumanensis* scats, but only four samples were involved. *Lasionycteris noctivagans* had more lepidopterans in scats than in stomachs (64.6 vs. 22.7 percent by volume); but coleopterans, homopterans, and hymenopterans were underrepresented in scat samples. On the other hand, hemerobiids were important in scats, but not in stomachs. Lepidopterans are one of the forms that would be expected in greater volume in scats than in stomachs because of differential digestion—scales do not digest. Indeed, with one exception, lepidopterans formed a greater percentage volume of scat material than of stomach material (in six of the seven bat species in which both scats and stomachs were available for comparison). Coleopterans are another group that would be expected in greater percentage volume in scats than in stomachs because of the chitinous parts, but coleopterans were more abundant in stomachs (in six of the seven bat species for which we had both stomach and scat samples).

Homopterans and dipterans are relatively soft and therefore would be expected to be more abundant in stomach material than in scat material. Homopterans were in greater volume in scats in three bat species, and in stomachs in four bat species. In two of the latter species (*Myotis volans* and *Lasionycteris noctivagans*), however, the differences were considerable, and may have shown the effects of differential digestion. Dipterans were found in greater volumes in stomachs of three bat species and in greater volumes in scats of four bat species.

## Summary

Examination of the data suggests that interspecific partitioning of the food resource

exists, despite the dietary overlap, particularly within lepidopterans. In addition, bats feed at different times, at different heights above the ground, in different areas of a specific habitat, and tend to select for certain groups of prey species. That lepidopterans were so important in the bats' diet undoubtedly reflects the lepidopterans' abundance. Were it possible to separate the lepidopteran taxa, differences in prey species selection by the bat species would probably become clear.

Scat analysis may show some effects of differential digestion, perhaps with overestimation of some foods, such as lepidopterans, and underestimation of some foods, such as homopterans. One therefore may be led astray in specific cases.

Although stomach analysis is probably still best, results from those species with adequate sample sizes indicate that scat analysis may be accurate enough to be used as a technique for comparison of food habits. Further work, with bats collected at the same time and place, is necessary for a detailed comparison.

**Acknowledgments**

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# Some Aspects of the Breeding Ecology of the Great Blue Heron at Heyburn State Park

**Abstract**

Reproductive information was gathered on the Great Blue Heron (*Ardea herodias*) at Heyburn State Park. Onset of the breeding season was 1 March 1977 and 25 February 1978; breeding terminated in the first half of August each year.

Fledglings were counted in 109 nests in 1977 and 148 in 1978; 2.14 and 2.20 were produced per successful nest. The 1.95 young per nesting pair in 1978 is believed adequate to maintain stable population. Nestling mortality was highest during the two to four weeks after hatching in 1977 and four to six weeks in 1978. Overall, nestling mortality was 18 percent in 1977 and 19 percent in 1978; starvation of young was the chief mortality factor.

## Introduction

In northern Idaho, productivity and distributional information on the Great Blue Heron is not available. Heronries at Cocalalla Lake (estimate 200 individuals), Swan Lake (28 nest structures, 1972), Heyburn State Park (69-106 active nests, 1970-72) (Dr. Donald R. Johnson, University of Idaho, pers. comm.), and Mica Bay (15 active nests, pers. obs., 1978) have received only brief investigation.

Information is presented here on the breeding ecology of the Great Blue Heron at the Heyburn State Park Heronry, Benewah County, Idaho.

## Study Area and Methods

The heronry was located on a mountain ridge about 640 m above sea level in the eastern portion of Heyburn State Park (Fig. 1), and occupied an area of approximately 11,000 $m^2$. The St. Joe River and Benewah Lake, about 0.4 km and 0.7 km away, respectively, were the nearest feeding grounds. Nests were built in *Pinus ponderosa* (69 percent), *Abies grandis* (14 percent), and *Larix occidentalis* (17 percent). Nest height ranged from 20-40 m.

The field work was conducted from February to August of 1977 and 1978. All trees with visible active nests were marked with numbered plywood plates and then plotted on a chart. In addition, one nest was arbitrarily assigned to each tree in which nests were not visible but nesting activity was evident (sound, whitewash, egg shells on the ground). Nesting success is reported as the mean number of young per nesting pair and as the mean number of young per successful nest at nine weeks of age. Pratt (1970) reported that nestlings abandoned nests as early as 64 days after hatching. Whenever possible, nests were observed from the ground or from heights of about 30 m in nearby trees. Counts of visible young were made once a week after hatching

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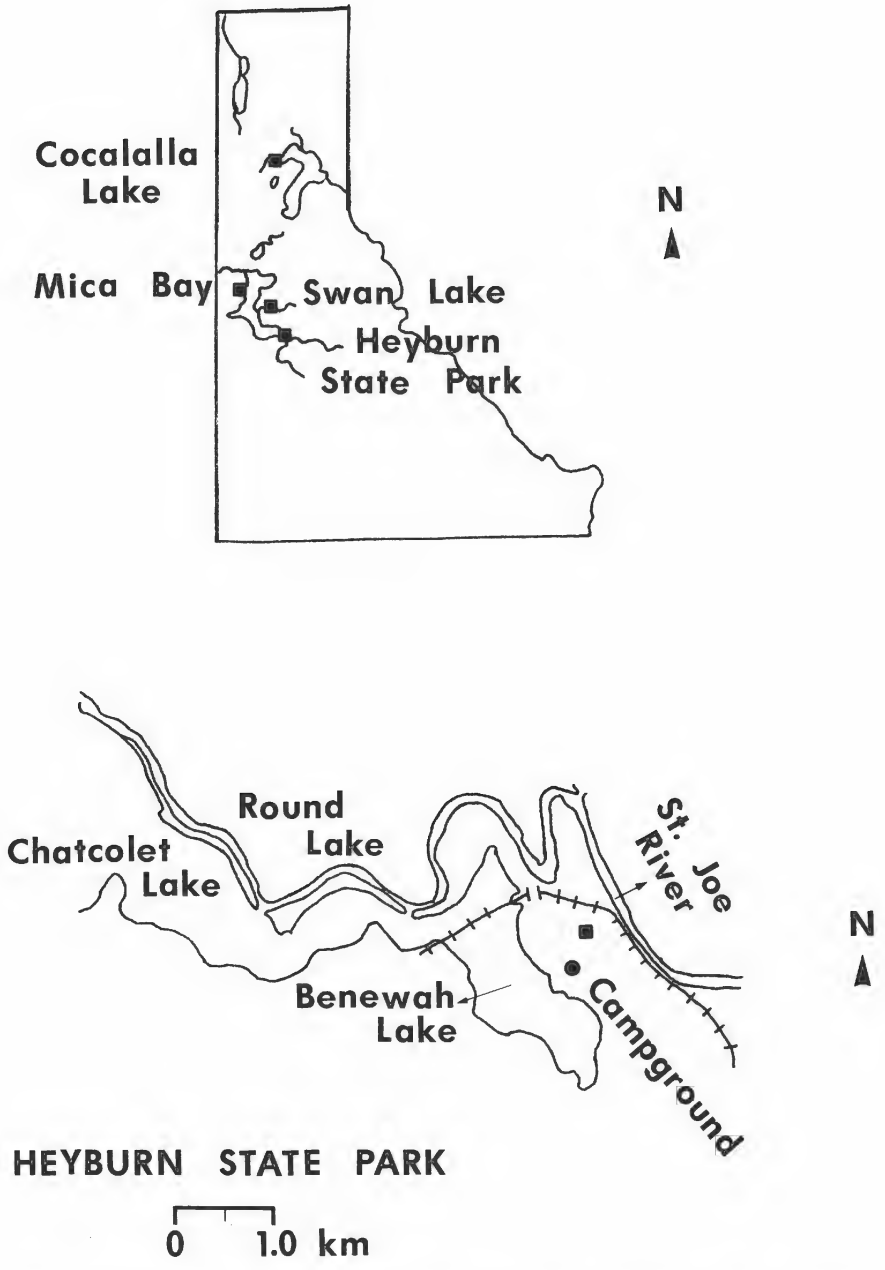


Figure 1. Distribution of Great Blue Heron heronries in northern Idaho and Heyburn State Park heronry location. ■ = heronry.

for both seasons. Dead nestlings were examined to ascertain possible causes of mortality and approximate age at death.

### Results and Discussion

Herons were first observed at the heronry on 1 March 1977 and 25 February 1978. The first egg shells from hatched eggs were found on 23 April 1977 and 18 April 1978. Incubation, which commences after the first or second egg has been laid (producing asynchronous hatching), lasts 25-29 days (Pratt, 1970). Thus, the first eggs were probably laid during the week of March 20th in both years. The last nestlings fledged in the first half of August each year.

Fledglings were counted in 109 nests in 1977 and 148 in 1978 (Table 1). Fledging number was two (mode) both years and there was no significant difference between years in the distribution of number of nests fledging one to four nestlings ($X^2 = 0.0550$; $P > 0.05$). Miller (1943), Vermeer (1969), and Pratt (1970, 1972) reported similar fledging rates. This heronry produced 1.95 young per nesting pair in 1978; this number is above the production believed necessary to maintain a stable population in the northern United States (Henny, 1972). The mean number of young fledged per successful nest was 2.14 in 1977 and 2.20 in 1978. An estimated 12 pairs in 1977 and 8 in 1978 from trees with non-visible nests were presumed to have been successful; assuming that each pair fledged two young, the mean number of young per successful nest would have been 2.12 in 1977 and 2.18 in 1978. Productivity rates in this paper compare closely to other values in the Pacific Northwest (Table 2).

A total of 51 (18 percent) nestlings in 1977 and 76 (19 percent) in 1978 were found dead on the ground. Since the initial brood size could not be determined for either season, these values must be considered conservative. Some nestlings may have been lost to predators or remained unseen due to the dense foliage in some nestling trees. The proportion of successful nests fledging only one nestling (24 and 23 per-

TABLE 1. Fledging success of Great Blue Herons at Heyburn State Park, northern Idaho.

| No. fledgling per active nest | No. of nests 1977 | 1978 |
|---|---|---|
| 0 | — | 19 |
| 1 | 26 | 34 |
| 2 | 48 | 64 |
| 3 | 29 | 39 |
| 4 | 6 | 9 |
| 5 | 0 | 2 |
| Total nestlings | 233 | 325 |

TABLE 2. Summary of reproductive success for the Great Blue Heron in the Pacific Northwest.

| Location | Year | No. young fledged per successful nest | No. young fledged per nesting pair | Source |
|---|---|---|---|---|
| Western Oregon | 1970 | 2.61 | 2.04 | Henny & Bethers (1971) |
| Western Oregon | 1974 | 2.18-2.70 | —— | Werschkul et al. (1977) |
| Northwestern Oregon | 1975 | 2.32 | 1.96 | English (1978) |
| Northern Idaho | 1977 | 2.14 | —— | This study |
| Northern Idaho | 1978 | 2.20 | 1.95 | This study |

cent) seems high because clutch size in the Great Blue Heron is typically four (Henny, 1972); this figure may be the result of high egg loss, hatching failure, or early death of nestlings. Werschkul *et al.* (1977) attributed low fledging success to human disturbance in Oregon. Although no evidence of nestling mortality due to disturbance from trains or the numerous visits by vacationers and field parties was found in this heronry, it is possible that such disturbances might have had detrimental effects during the pre-hatching period (i.e., lower clutch size) similar to those reported on other aquatic birds (Schreiber, 1979; Robert and Ralph, 1975). It is also possible that an unusually high number of young, inexperienced pairs occurred in this colony.

Approximate age at death was recorded for 29 nestlings in 1977 and 60 in 1978. The highest mortality occurred during the two to four week period after hatching in 1977 and during the four to six week period in 1978 (Table 3). I found starvation of the young to be the greatest cause of mortality in this heronry. Pratt (1970, 1972) and Kushlan (1978) reported that the greatest cause of mortality was starvation of the younger, smaller chicks due to their inability to compete for food with older siblings.

TABLE 3. Nestling mortality relative to age.

| Weeks | No. Dead 1977 | 1978 |
|---|---|---|
| 0-2 | 8 | 7 |
| 2-4 | 12 | 17 |
| 4-6 | 6 | 19 |
| 6-8 | 2 | 8 |
| 8-10 | 1 | 7 |
| 10- | 0 | 2 |

Other causes of mortality were an irregular piece of fish bone obstructing the esophagus of nestlings, nestlings falling while struggling for food, and nest structures falling from trees. Altogether, accidental deaths killed five nestlings (10 percent) in 1977 and nine (12 percent) in 1978. Seven of the nine nestlings found dead in 1978 occurred four to six weeks post-hatch. Avian predation was not observed, although young and adults were harassed by Ospreys (*Pandion haliaetus*) on four occasions.

Additional work is needed in this heronry to determine percent egg and hatching failure and early nestling mortality. A survey of heronry locations throughout northern Idaho would be valuable. Heronries of various sizes would provide an adequate sample size to test the suspected relationship between colony fledging success and several important factors defined by Werschkul *et al.* (1977). In addition, these heronries could provide additional information regarding the "Information Center" hypothesis (Krebs, 1974).

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# Small Mammal Populations on the Kenai Peninsula, Alaska

## Abstract

During May to September 1974, 298 small mammals of six species (two soricids and four microtines) were captured during 34,609 trapnights (8.6 mammals/1000 tn) on the Kenai National Moose Range, Alaska. Capture success increased sixfold with increases in elevation and ninefold through the summer. Compared with studies in other years, capture success was low in all areas. Timberline areas had greatest species diversity; several species were limited in geographic distribution. Five additional species potentially or known to be present were not captured.

## Introduction

The occurrence of fluctuations in small mammal populations in North America has been well documented (Krebs and Meyers, 1974). The ecological and geographic distribution of some sympatric or adjacent populations of soricids and microtines has also been reported (Getz, 1961; Brown, 1967). Studies were conducted during May to September 1974 to determine the relative abundance and distribution of small mammals on the Kenai National Moose Range, Alaska. This paper reports on the apparent population fluctuations occurring there in recent years, and the influence of elevation on relative numbers and distribution.

## Study Area

The Moose Range is located in the northwestern part of the Kenai Peninsula on the southcentral coast of Alaska (Fig. 1). The Range is bounded by Cook Inlet on the north and west, and the Kenai Mountains (up to 2000 m above sea level) on the south and east. The area is characterized by two distinct physiographic features: the forested, lake-dotted lowlands, and the treeless benches and mountains.

The vegetation in the lowlands, which comprise the northwestern two-thirds of the Range, varies from black spruce (*Picea mariana*) muskegs to climax white spruce (*P. glauca*); birch (*Betula spp.*), aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and willows (*Salix* spp.) are present as pure stands or mixed with spruce. Common understory species include alder (*Alnus crispa*), *Vaccinium* spp., fireweed (*Epilobium angustifolium*), bunchberry (*Cornus canadensis*), crowberry (*Empetrum nigrum*), willow, and *Sphagnum* spp. Parts of the lowland area have burned in recent years (1250 km$^2$ in 1947 and 350 km$^2$ in 1969) and are in varying stages of succession. In the treeless alpine tundra areas, common vegetation includes dwarf birch (*B. glandulosa*), bearberry (*Arctostaphalus uva-ursi*), blueberry and willow, and alder near lakeshores.

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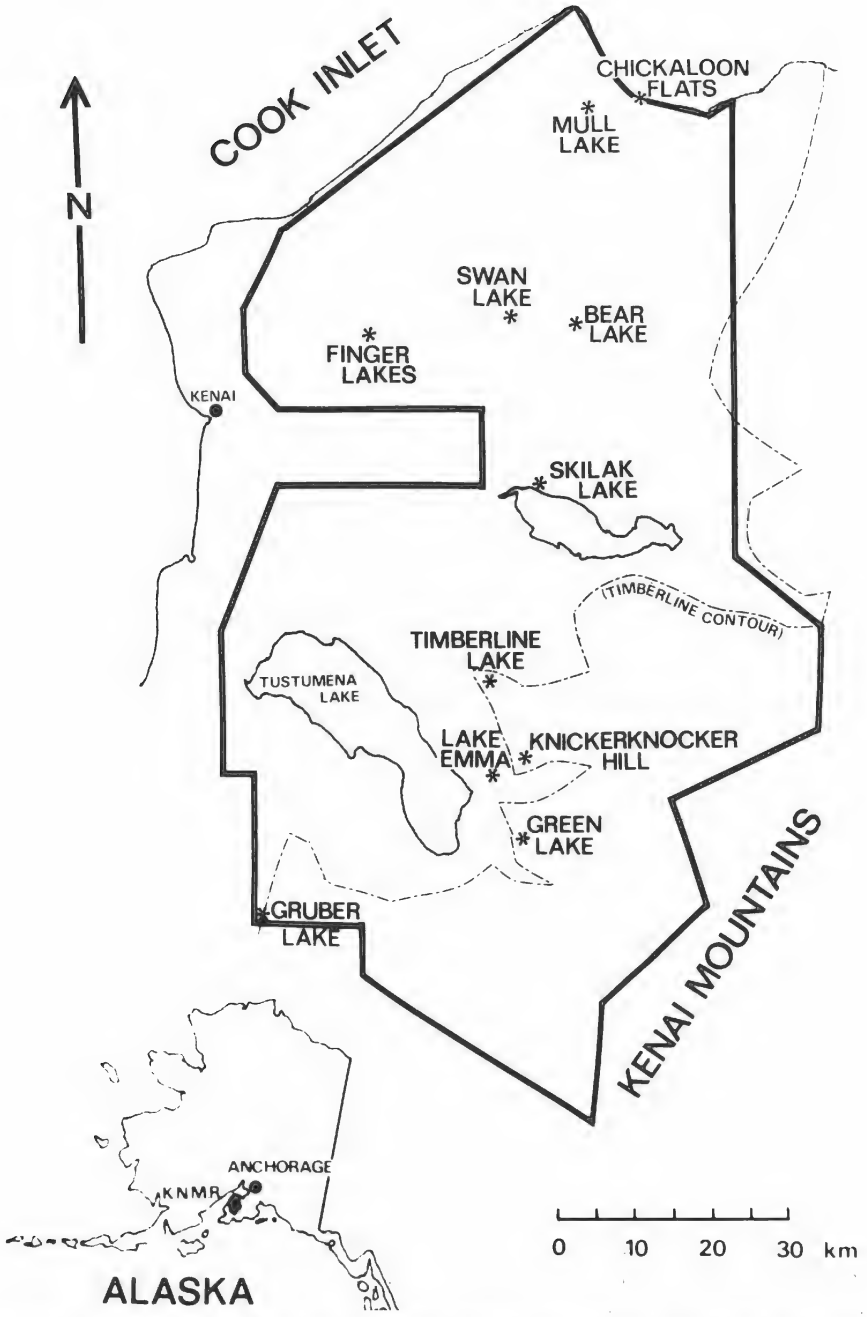


Figure 1. Locations on the Kenai National Moose Range, Alaska, where trapping for small mammals was conducted 18 May-24 September 1974.

The mean elevation of six lowland study areas is 74 m (range 3-121 m). Part of the Finger Lakes area (Fig. 1) is in the 1969 burn, and parts of both the Bear Lake and Swan Lake areas are in the 1947 burn. Much of the Mull Lake area is located in virgin birch-spruce forest; the Chickaloon Flats encompass an unburned island-tidal area, and the Skilak Lake area is in mature aspen and spruce forests. The elevation of the three alpine tundra study areas, Green Lake, Timberline Lake, and Knickerknocker Hill, averages 662 m (range 472-848 m). The other two study areas, Lake Emma and Gruber Lake, average 424 m in elevation (range 318-530 m), and include areas at or to 200 m below timberline.

#### Methods

Each study area was investigated for seven to fourteen days; four areas (Finger Lakes, Swan Lake, Skilak Lake, and Timberline Lake) were investigated twice. During May and June, small mammal capture attempts were made with about 250 snap traps (mostly Museum Specials, but also a few Victor mouse and rat traps), and 250 Sherman folding live traps. With the acquisition of an additional 250 Museum Special traps in late June, such traps were used exclusively from July through September. Traps were baited with a mixture of peanut butter and bacon grease. They were spaced approximately 8 m apart and set out in lines of 30 each. Lines were placed in representative habitat types where prospects for capture success looked promising. Traps were checked each morning, and lines moved to new areas every two to four days. As many forest types as possible were sampled in each area.

The skins, skulls, and reproductive tracts of captured animals were saved, and weights and body measurements recorded. Species were identified by skull, pelage, and body characteristics (Hall and Kelson, 1959).

#### Results

Six species of small mammals were captured from 18 May to 4 September 1974: vagrant shrew (*Sorex vagrans*), masked shrew (*S. cinereus*), singing vole (*Microtus miurus*), tundra vole (*M. oeconomus*), northern red-backed vole (*Clethrionomys rutilus*), and northern bog lemming (*Synaptomys borealis*). A total of 298 captures was made during 34,609 trapnights, an average of 8.6 individuals/1000 trapnights (Table 1). Red-backed voles were most commonly caught (3.9/1000 trapnights); vagrant shrews and bog lemmings were captured least often (0.1/1000 trapnights).

Significant differences in the relative number of animals caught were noted with respect to both elevation and time of year (Table 1). During July and August relatively twice as many individuals of all species were captured in timberline areas than in lowland forest areas, and more than six times as many were caught in alpine tundra areas. Differences in capture success for each species were most notable in alpine tundra as opposed to other areas. In addition, lowland areas trapped during July-August and September yielded four and nine times, respectively, the number of individuals captured per 1000 trapnights there during May-June.

Timberline areas produced the greatest species diversity; all six species were found there (Table 1). No vagrant shrews or bog lemmings were found in alpine tundra areas, and no bog lemmings and only one *Microtus* were taken from lowland forest areas. Red-backed voles were common in all areas, as were masked shrews.

TABLE 1. Capture success and distribution of six small mammal species trapped on the Kenai National Moose Range, Alaska, during 18 May to 4 September 1974. Range of capture success shown in parentheses.

| Habitat | Months | Study areas[a] | No. of each species captured[b] | | | | | | | No. of trapnights | Total no. of captures/ 1000 trapnights |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | S.v. | S.c. | M.m. | M.o. | C.r. | S.b. | Total | | |
| Lowland forest | May-Jun | Fn,Be,Sw,Fn,Sw,Sk | | | | | 17 | | 17 | 16,037 | 1.1(0.0-2.2) |
| | Jul-Aug | Fn,Sw,Sk | 3 | 9 | | 1 | 16 | | 29 | 6,103 | 4.8(2.9-6.3) |
| | Sep | Sk | | 1 | | | 12 | | 13 | 1,261 | 10.3 |
| Timberline | Jul-Aug | Em,Gr | 1 | 6 | 16 | 23 | 13 | 5 | 64 | 5,390 | 11.9(10.4-13.8) |
| Alpine tundra | Jul-Aug | Gn,Tm,Kn,Tm | | 16 | 19 | 64 | 76 | | 175 | 5,818 | 30.1(2.1-61.1) |
| | | Total | 4 | 32 | 35 | 88 | 134 | 5 | 298 | 34,609 | 8.6 |

[a]Fn—Finger Lakes; Be—Bear Lake; Sw—Swan Lake; Mu—Mull Lake; Ch—Chickaloon Flats; Sk—Skilak Lake; Em—Lake Emma; Gr—Gruber Lake; Gn—Green Lake; Tm—Timberline Lake; Kn—Knickerknocker Hill.

[b]S.v.—Sorex vagrans; S.c.—Sorex cinereus; M.m.—Microtus miurus; M.o.—Microtus oeconomus; C.r.—Clethrionomys rutilus; S.b.—Synaptomys borealis.

## Discussion

Small mammals were apparently very abundant on the Moose Range during summer 1973, judging from the number of inquiries concerning "mouse" damage made to the Moose Range staff, and the observations of naturalists and outfitters in the area (J. Monnie and B. Schaeffer, pers. comm.). Thus, it seems likely that a population crash occurred during winter 1973-74; this hypothesis was reflected in the low number of animals caught in summer 1974. Data from other researchers indicate the relative abundance of small mammals in lowland forest areas on the Peninsula in other years. Trap success near Finger Lakes in 1970 ranged from 31-83/1000 trapnights (Ellison, 1970). During summers 1977 and 1978, Bangs (1979) averaged 89 captures/1000 trapnights in vegetationally disturbed and undisturbed sites; success varied from 66-103/1000 trapnights. Compared to our unweighted mean capture success for May-September of 5.4/1000 trapnights in lowland areas, these values reflect a six- to sixteenfold difference. This magnitude of change has been reported elsewhere for a red-backed vole population (Patric, 1962), and is not uncommon for microtines (Krebs and Meyers, 1974).

Seasonal increases in small mammal numbers are to be expected. The initiation of reproduction in spring and continued recruitment through summer would most obviously be involved. Also, change in trap type may have contributed to an increased number of captures in lowland areas after June.

Altitudinal differences in trapping success most likely reflected differences in habitat quality and/or quantity, and thus carrying capacity. However, these differences may also reflect cycle asynchrony of allopatric populations.

Bangs (1979) found, as we did, that red-backed voles and masked shrews were the dominant species in lowland forest areas. He also captured several bog lemmings and vagrant shrews there, as well as two species we did not capture: meadow voles (*Microtus pennsylvanicus*) and pygmy shrews (*Microsorex hoyi*). That no singing or tundra voles were captured in lowland areas concurs with our data. The absence of meadow voles in our sample may reflect the presumably low population in 1974, combined with low trapping effort in grassy areas in which *M. pennsylvanicus* might have been more abundant. With regard to pygmy shrews, the fact that both Bangs (1979) and Brown (1967) reported lower shrew trapping success with conventional non-modified snap traps is noteworthy. Because of their small size, capture success of pygmy shrews would likely be affected. Sunken can traps provide higher capture success of shrews (Brown, 1967), and E. Bangs (pers. comm.) noted that success often increases after other species in the area are removed

Three other species of small mammals, water shrew (*Sorex palustris*), brown lemming (*Lemmus trimucronatus*), and meadow jumping mouse (*Zapus hudsonicus*), are potentially residents on the Kenai Peninsula, according to various range distribution maps (Hall and Kelson, 1959; Manville and Young, 1965). These accounts present no evidence of specimens collected on the Peninsula, and in light of the results of this study and the work of Bangs (1979), the presence of viable populations of these species remains suspect.

## Acknowledgments

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# Chigger Infestation of Humans in Washington, Involving Euschoengastia numerosa (Acari: Trombiculidae)

**Abstract**

A specimen of *Euschoengastia numerosa* Wrenn and Loomis was collected in a human case of apparent trombiculid infestation in Spokane County, Washington. The species was previously unrecorded for the state.

On 18 April 1979, a married couple, students at Whitworth College, Spokane, Washington, reported to Dr. David Stangland at the College Medical Center. They had been hiking about 30 km north of Spokane (Spokane County). The torsoes and extremities of both patients had numerous small papules. These were slightly pruritic, each with a small pore, and some with orange-colored centers. An ointment was prescribed and lesions were much improved within 48 hours.

An arthropod specimen was removed from one of the papules and sent to Eastern Washington University for identification. It was subsequently determined by G. W. Krantz, Oregon State University, Corvallis, Oregon, as *Euschoengastia numerosa* Wrenn and Loomis, a species previously unrecorded from Washington.

In the United States, recognized cases of parasitization of humans by chigger mites have been rare outside the ranges of *Trombicula alfreddugesi* (Oudemans) and *T. splendens* Ewing. However, according to Easton and Krantz (1973), occasional infestations of humans and horses by *Euschoengastia* sp. have occurred in Oregon.

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Easton, E. R., and G. W. Krantz. 1973. A *Euschoengastia* species (Acari: Trombiculidae) of possible medical and veterinary importance in Oregon. J. Med. Entomol. 10:225-226.

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# Ambrosia Fungi of the Western United States and Canada—Beetle Associations (Coleoptera: Scolytidae), Tree Hosts, and Distributions

## Abstract

Imperfect ambrosia fungi of the genera *Ambrosiella* and *Raffaelea* were found symbiotically associated with 11 species of wood-boring ambrosia beetles. *Raffaelea canadensis, R. sulcati, Ambrosiella brunnea, A. ferruginea, A. gnathotrichi, A. hartigii, A. sulcati,* and *A. sulphurea* were reported from 16 new tree hosts and extended their known distribution in the western United States and Canada.

## Introduction

The ambrosia fungi in this study are ectosymbionts of wood-boring Coleoptera of the families Scolytidae and Platypodidae. Ambrosia fungi are ectosymbiotic rather than endosymbiotic because they are externally cultivated and ingested by the symbiotic beetle and its progeny. However, the fungi are transmitted in special ectodermal organs called mycangia (Franke-Grosmann, 1967). In temperate regions ambrosia beetles infest the xylem cylinder of weakened or logged trees and propagate the ambrosia fungi upon the walls of a gallery system which they excavate in the wood.

The general biology of ambrosia beetles and their fungi has been reviewed by Franke-Grosmann (1967) and Norris (1979). The taxonomy and cultural descriptions of ambrosia fungi collected in this report utilized the studies of Batra (1967), Funk (1970), and Roeper *et al.* (1980). This study reports the association of eight ambrosia fungi with 11 ambrosia beetle species in the western United States and Canada with particular reference to new tree host associations and distribution.

## Methods

During their brief flight period, ambrosia beetles aggregate near timber at saw mills, logging operations, wind-thrown trees, or diseased trees. They were collected in flight with a hand net or a mechanized rotary trap net (Daterman *et al.*, 1965). Large pieces of timber were taken to the laboratory and dissected to remove beetles or fungi from galleries. Examination and isolations were made within one day of collection except when materials had to be transported more than 300 mi.

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Mycangia from *Trypodendron* and *Xyleborus* species were removed from the female adults by dissecting the beetle in a series of drops of sterile water on a sterile glass slide (Batra, 1963). The mycangium was separated and rinsed in sterile water; it was either crushed directly onto agar or its contents were squeezed onto agar. Fungi were isolated from the coxal mycangia of *Gnathotrichus* males or *Monarthrum* females either by complete dissection as above or by killing the beetle, placing it on its back, removing the coxa, lifting out the fungal mass with a fine needle, and placing the fungus on agar medium (Funk, 1970). The pit-like mycangia of *Platypus wilsoni* Swaine females were removed, washed in sterile water, cut into small pieces, and placed on the surface of the agar medium. In all isolations the beetles were cleaned externally by alternating 12-hr exposures to wet and dry sterile filter paper (Batra, 1963).

Ambrosia fungi were isolated from galleries immediately after splitting the galleries open. Isolations were made primarily from the fungal growth which lined the tunnel walls or larval niches upon which active larvae or adults were feeding. Single point inoculations and streaks on agar media were made from each gallery. If noticeable fungal material was lacking, wood slivers were plated.

All the isolation media were solidified with 2.0 percent agar and sterilized by autoclaving. Media used were: 3.0 percent malt extract agar, 3.0 percent malt extract and 1.0 percent yeast extract agar, 0.6 percent malt extract agar, and potato dextrose agar and 0.6 potato dextrose agar. Following isolation from single fungal colonies or hyphal tips of filamentous fungal colonies, the isolated fungi were subcultured on 3.0 percent malt extract and 1.0 percent yeast extract agar and maintained until examined.

## Results

*Raffaelea canadensis* Batra

Isolations made from mycangia of female adults of *Platypus wilsoni* Swaine and galleries: RAR-297 A & B, *Tsuga heterophylla* (Raf.) Sarg., Lost Prairie Campground, Willamette Nat. Forest, Oregon, 26 VI 1970; RAR-315, *Pseudotsuga menziesii* (Mirb.) Franco, Dunn State Forest, Oregon, 1 X 1970; RAR-322, Dawson, Oregon, 15 X 1970, from mycangia of adult female collected in flight.

Originally described as *Tubercularia ambrosiae* Funk when collected from *P. wilsoni* infesting *P. menziesii* on Vancouver Island, B.C. (Funk, 1965). Batra (1967) placed this fungus in the genus *Raffaelea* and provided a redescription. *T. heterophylla* (Raf.) Sarg. recorded here as new host and distribution to Oregon.

*Raffaelea sulcati* Funk

Isolations made from mycangia of adult male of *Gnathotrichus sulcatus* LeConte and galleries: RAR-115a, Harlan, Oregon, 1 X 1962 from mycangia of flight adult; RAR-125 A & B, *P. menziesii*, 3 mi. S.W. of Harlan, Oregon, 7 X 1969; RAR-237 A & B, *T. heterophylla*, Mary's Peak, Oregon, 2 I 1970; RAR-403 A & B, *Thuja plicata* Don., Golden, B.C., Canada, 9 XII 1971.

Funk (1970) described this fungus collected from *G. sulcatus* infesting *P. menziesii* on Vancouver Island, B.C. Tree hosts *T. heterophylla* and *T. plicata* and distribution to Oregon were recorded here as new.

*Ambrosiella brunnea* (Verrall) Batra

Isolations from mycangia of adult females of *Monarthrum scutellare* LeConte and galleries: RAR-361, *Quercus garryana* Dougl., Alsea, Oregon, 4 IV 1971; RAR-370 A & B, *Umbellularia californica* (Hook & Arn) Nut., Saratoga Springs, Cal., 10 VII 1971; RAR-389 A & B, *Q. lobata* Nee, 1 mi. E. of Castle Rock State Park, Cal., 13 VII 1971; RAR-373 A & B, *Q. agrifolia* Nee, Saratoga Springs, Cal., 14 VII 1971. Isolated from mycangia of adult females of *M. dentiger* LeConte and galleries: RAR-332. *Q. agrifolia*, Castle Rock State Park, Cal., 11 XI 1970; RAR-374 A & B, *Q. agrifolia*, ½ mi. E. of Castle Rock State Park, Cal., 13 VII 1971; RAR-376 A & B, *Q. lobata*, ½ mi. E. of Castle Rock State Park, 13 VII 1971; RAR-407, *Q. agrifolia*, Saratoga Springs, Cal., 15 VII 1971.

Verrall (1943) originally described this fungus as *Monilia brunnea* associated with *Monarthrum* species infesting *Quercus* in Mississippi. Batra (1967) placed this fungus in *Ambrosiella*, associating it with both *M. fasicatum* Say and *M. mali* Fitch infesting *Quercus* species in eastern U.S.A. Funk (1965) isolated the fungus from *M. scutellare* which infested *Q. garryana* in British Columbia. Association with *M. dentiger* has been previously reported (Roeper and French, 1978). *Q. lobata, Q. agrifolia*, and *U. californica* are here reported as new hosts and California and Oregon as new distributions.

*Ambrosiella ferruginea* (Mathiesen-Kaarik) Batra

Isolations were made from mycangia of adult females of *Trypodendron lineatum* Olivier and their galleries: RAR-256, A & B, *P. menziesii*, Lewisburg Ridge, Oregon, 15 VII 1969; RAR-267, Mary's Peak, Oregon, 24 IV 1970, from mycangium of flight adult female; RAR-275 A & B, *Picea excelsa* Link, Cascade Head Exper. Forest, Oregon, 24 V 1970; RAR-277 A & B, *T. heterophylla*, Cascade Head Exper. Forest, Oregon, 25 V 1970; *Pinus contorta* Doug., Pringle Falls, Oregon, 29 V 1970; RAR-299, *Picea engelmannii*, Salie Falls, Oregon, 10 VII 1970 from mycangia only. Isolations made from mycangia of adult females of *T. retusum* LeConte and galleries: RAR-282 A & B, *Populus tremuloides* Michx., Indian Springs, Oregon, 2 VI 1970; RAR-406 A & B, *P. tremuloides*, Alsike, Alberta, 2 VII 1971; RAR-411, *P. tremuloides*, 2 mi. E. of Steamboat Springs, Colorado, 7 VIII 1971, from mycangia only. Isolations made from mycangia of adult females of *Trypodendron rufitaris* Kirby: RAR-309 A & B, *P. contorta*, Odell Lake, Oregon, 13 VIII 1970; RAR-330, *Polyporus schweinitzii*, Priest Lake, Idaho, 12 X 1970, from hibernating adult female. Isolations made from mycangium of *T. betulae* Swaine: RAR-405, *B. papyrifera* March (Rydb.) Sarg., Alsike, Alberta, 3 VII 1971.

Hartig (1872), who was probably first to observe *A. ferruginea*, suggested that the fungus growing on walls of the galleries of *T. lineatum* was the principal food for both larvae and adults. Leach *et al.* (1940) also observed the fungus but did not name it. Mathiesen-Kaarik (1953) provided a formal taxonomic description, naming the fungus *Monilia ferruginea.* Batra (1963) and Funk (1965) isolated *M. ferruginea* from the mycangia of *Trypodendron species.* Batra (1967) transferred the fungus to the genus *Ambrosiella.* French and Roeper (1972) reported the association of *T. rufitarsis* with *A. ferruginea. P. sitchensis, P. contorta*, and *T. heterophylla* are recorded here as new hosts and distribution is extended to Alberta and Idaho.

*Ambrosiella gnathotrichi* Batra

Isolations made from the mycangia of adult males of *Gnathotrichus retusus* LeConte and gallery: RAR-27, Mary's Peak, Oregon, 11 VI 1969 from flight adult; RAR-88 *P menziesii*, Mary's Peak, Oregon, 20 VIII 1969 from larval niche only; RAR-294, Mary's Peak, Oregon, 21 V 1970, from flight adult; RAR-327, Harlan, Oregon, 11 X 1970; from flight adult.

Batra (1967) described this fungus from *G. retusus* attacking *Pinus* sp. in Colorado. Roeper *et al.* (1980) have previously noted association of this fungus with *G. materiarus* Fitch in Michigan. *P. menziesii* reported here as new host and distribution extended to Oregon.

*Ambrosiella hartigii* Batra

Isolations made from mycangia of adult females of *Xyleborus dispar* Fabricius and galleries: RAR-280 A & B, *Prunus avium* L., Corvallis, Oregon, 30 IV 1970; RAR-286 A & B, *Alnus rubra* Bong, Mary's Peak, Oregon, 1 V 1970; RAR-287 A, Lewisberg Ridge MacDonald Forest, Oregon, 2 V 1970, from mycangium of flight adult; RAR-290 A, Dawson, Oregon, 10 V 1970, from mycangium of flight adult; RAR-305 A & B, *P. avium*, Salem, Oregon, 3 V 1970; RAR-317 A & B, *P. avium*, Salem, Oregon, 10 IX 1970; RAR-318 A & B, *Malus sylvestris* Mill., Hood River, Oregon, 1 X 1970; RAR-319 A & B, *M. sylvestris*, White Salmon, Washington, 1 X 1970; RAR-413, *P. avium*, Salem, Oregon, 1 VIII 1971.

Originally described as *Monilia candidia* by Hartig (1844) associated with *X. dispar* in Germany. Batra (1967) redescribed as *A. hartigii* associated with *X. dispar* also from Germany. Roeper *et al.* (1980) have noted associations of this fungus with *X. sayi* Hopkins and *X. obesus* LeConte in Michigan. *A. rubra* and *P. avium* reported here as new hosts and distribution is extended to Oregon and Washington.

*Ambrosiella sulcati* Funk

Isolations made from mycangia of adult males of *Gnathotrichus sulcati* LeConte and gallery: RAR-119, 3 mi. S.W. of Harlan, Oregon, 10 X 1969, from flight adult; RAR-137, Harlan, Oregon, 14 X 1969, from flight adult; RAR-250, *P. menziesii*, Mary's Peak, Oregon, 10 VII 1969.

*A. sulcati* was described by Funk (1970) from *G. sulcati* from Vancouver Island, B.C. These collections represent extension of range to Oregon.

*Ambrosiella sulphurea* Batra

Isolations made from mycangia of adult females of *Xyleborus saxeseni* Ratzeburg and galleries: RAR-283 A & B, *Prunus avium* L., Corvallis, Oregon, 12 X 1970; RAR-321, *P. avium*, Salem, Oregon, 12 X 1970; RAR-324, *Acer macrophyllum* Pursh, Sulphur Spring, Oregon, 12 X 1970; RAR-331 A & B, *A. macrophyllum*, Saratoga Springs, Cal., 5 XI 1970; RAR-361, *Q. garryana*, Alsea, Oregon, 15 X 1970; RAR-399 A & B, *M. sylvestris*, Hood River, Oregon, 5 VI 1971.

Batra (1967) described *A. sulphurea* associated with *X. saxeseni* from Kansas. Roeper *et al.* (1980) also isolated this fungus from *X. saxeseni* in Michigan. *Q. garryana, A. macrophyllum, P. avium*, and *M sylvestris* are here recorded as new hosts.

The range of *A. sulphurea* is extended to western United States with collections from California and Oregon.

### Discussion

Ambrosia fungi form a biological unit with their symbiotic beetles. A single fungal species can be associated with more than one beetle species (i.e., *A. brunnea, A. ferruginea*) and, conversely, a single beetle can be associated with more than one fungus (i.e., *G. sulcatus*). In this study, 16 new tree hosts were recorded for the ambrosia fungi without any changes in the specific beetle-fungal associations. In the symbiotic association, the ambrosia beetles and their fungi appear to act together and are generally "polyphagous" (Franke-Grosmann, 1967). The ambrosia fungus (fungi) did not appear to influence the host selection of its symbiotic beetle. For example, the beetles *T. retusum, T. betulae*, and *T. rufitarsis* have a limited host range, whereas *T. lineatum* has a wide host range (Wood, 1957). *A. ferruginea* is associated with all of these *Trypodendron* species. Likewise, *A. brunnea* appears to have wider host range than the more limited host range of each of the *Monarthrum* species. The geographical distribution of an ambrosia fungus is apparently governed by the host range of its symbiotic beetle(s) and not vice versa.

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## ANNOUNCEMENT

The Northwest Scientific Association and the Editorial Board are pleased to announce that

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The following reprint and page charges for Northwest Science will be effective for all papers printed after 1 January 1982:

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In addition, the Trustees and Members approved an increase of individual and institutional memberships for 1982. Regular memberships will be $14 and student membership will be $8. A $1 discount will be given for membership paid before January 15.

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Donald R. Satterlund, Editor

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